Individual Variation in Prosociality of Group-living Common Marmosets: Assessing the Role of Oxytocin and Social Bonding

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To my parents,

with all my love

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II Thesis Abstract

Among primates, callitrichid monkeys such as common marmosets (*Callithrix jacchus*) stand out by their high levels of social tolerance, prosociality, and within-group cooperation. Their distinctive feature is the joint care for offspring, in which both the dominant breeding pair as well as non-reproductive helpers are involved. The need to cooperate closely to guarantee reproductive success presumably developed hand in hand with increased species-specific levels of social tolerance and prosocial motivation. Nevertheless, individuals also vary strongly in their prosocial performance and cooperativeness. This may be partly explained by diverging sex- and status-specific strategies, but other factors shaping individual prosociality at the more proximate level have barely been studied so far. Particularly relevant in this context is the role of social relationships that may influence individual cooperativeness, and the hormonal regulation of both social bonding and individual cooperativeness. The neurohormone oxytocin (OT) is a prominent candidate, since it is crucially involved in social bonding, care-taking behavior as well as the mediation of prosocial and cooperative interactions among adults in mammals.

The overall aim of my PhD thesis was to investigate the interaction of OT and social bonding in the regulation of individual prosocial behavior in group-living marmosets, especially with regard to infant-care. First, I assessed the structure and stability of social relationships in marmoset family groups by monitoring individual urinary OT levels and dyadic affiliative interactions over two distinct study periods. I found that individual OT responses to affiliation are partner-specific, i.e. strongly bonded marmoset partners showed synchronized longitudinal OT levels (chapter 2). Furthermore, I found that these patterns of dyadic affiliation and dyadic OT synchrony as well as individual group integration were stable over at least 6 months (chapter 3). Together, these findings suggest a differentiated and stable relationship structure in marmoset groups. Second, I tested the link between urinary OT and individual infant-care behavior and motivation in groups with dependent offspring. I could show that individual OT increased directly after the birth of a new litter, and that OT is positively linked to care-taking behaviors, in particular those likely to reflect intrinsic prosocial motivation (proactive food sharing). In contrast, no such link was found with behaviors that involve high physical contact (infant-grooming and carrying). This suggests that OT is particularly involved in the regulation of prosocial motivation (chapter 4). Finally, I investigated the influence of relationship quality and

dyadic grooming (as potential payment for help or infant-access) on individual infant-care behavior. Here, I found that mutual relationship quality rather than strategically directed grooming is relevant for individual care-taking contribution in breeding pairs and breeder-male helper dyads, which are usually the most important caretakers. In particular, relationship quality prior to birth predicted contribution to care-taking once the infants were born (chapter 5).

Overall, my findings highlight the key role of OT in the regulation of social relationships and prosocial behavior in marmoset family groups, and they emphasize the influence that these relationships themselves in turn have on individual cooperativeness. This pattern also strongly suggests that the broad behavioral impact of OT may be a consequence of interactions and cross-effects between different spheres of influence of OT, such as partner-specific bonding, prosocial infant-care, and overall within-group cooperation and coherence. Hence, this PhD thesis substantially contributes to the understanding of the proximate regulatory mechanisms underlying individual prosociality and successful cooperation during infant-care in callitrichid monkeys. My findings may thus also help to better understand cooperation and prosociality in humans, since humans and callitrichids are thought to share convergent adaptive prosocial traits due to cooperative breeding.

III Zusammenfassung

Innerhalb der Primaten zeichnen sich Krallenaffen, unter ihnen auch die Weissbüschelaffen, durch hohe Prosozialität und Kooperation innerhalb einer Gruppe aus. Ihr Alleinstellungsmerkmal ist die gemeinsame Aufzucht von Jungtieren in kleinen Familiengruppen, an der sich sowohl die dominanten Elternpaare als auch nicht-reproduktive Helfer beteiligen. Die Notwendigkeit zur engen Kooperation, um das Überleben des Nachwuchses zu sichern, ging in diesen Arten vermutlich mit der Entwicklung erhöhter sozialer Toleranz, prosozialer Motivation sowie verstärkter sozio-kognitiver Fähigkeiten und emotionaler Verarbeitung einher. Die Ausprägung prosozialen Verhaltens variiert jedoch stark zwischen Individuen, was zum Teil durch unterschiedliche sex- und status-spezifische Strategien erklärt werden kann. Andere Faktoren, die individuelles prosoziales Verhalten vor allem auf der proximaten Ebene regulieren, sind dagegen bisher kaum untersucht. In diesem Zusammenhang sind vor allem die sozialen Bindungen zwischen den Mitgliedern einer Gruppe von Bedeutung, da sie sich massgeblich auf das kooperative Verhalten der einzelnen Individuen auswirken können. Eine wichtige Rolle nimmt ausserdem die hormonelle Regulierung, sowohl von sozialen Bindungen als auch von prosozialem Verhalten selber (zum Beispiel dem Tragen von Jungtieren und Futter-Teilen), ein. Das Neurohormon Oxytocin ist dabei besonders relevant, da es in Säugetieren massgeblich an der Regulation von Bindungen, Brutpflegeverhalten sowie prosozialer und kooperativer Interaktionen beteiligt ist.

Das Ziel meiner Doktorarbeit war es, die Bedeutung und Interaktion von OT und sozialen Bindungen in der Regulation prosozialen Verhaltens in Gruppen-lebenden Weissbüschelaffen zu erforschen. Dabei habe ich zuerst untersucht, ob Weissbüschelaffen spezifische Bindungen mit anderen Gruppenmitgliedern eingehen, oder ob der Gruppenzusammenhalt eher durch den unspezifischen Austausch kooperativen und bindenden Verhaltens gewährleistet wird. Meine Annahme war, dass wenn Individuen Partnerpräferenzen unter den Gruppenmitgliedern haben, und besonders der affiliative Kontakt zwischen stark gebundenen Partnern erhöhte OT-Ausschüttung zur Folge hat, sich dies über die Zeit auch in individuellen basalen OT Levels widerspiegelt. In den Teilstudien 1 und 2 konnte ich diese Annahme bestätigen und zeigen, dass basale OT-Fluktuationen im Urin bei stärker gebundenen Partnern synchronisiert sind und dass sowohl diese partner-spezifischen OT-Muster als auch die Sozialstruktur in den Gruppen über

längere Zeit konsistent bleiben. Zusammengenommen sprechen diese Ergebnisse dafür, dass Weissbüschelaffen spezifische und stabile Bindungen miteinander eingehen.

Die dritte Teilstudie beschäftigte sich mit der Frage, inwiefern OT auch an der Regulation prosozialen Brutpflegeverhaltens beteiligt ist. Ich konnte zeigen, dass OT direkt nach der Geburt von Jungtieren bei allen Gruppenmitgliedern ansteigt und dass OT einen positiven Zusammenhang mit Formen der Brutpflege aufweist, die intrinsische prosoziale Motivation widerspiegeln (z.B. pro-aktives Futter-Teilen), jedoch nicht mit solchen, die eher durch starken physischen Kontakt mit den Jungtieren geprägt sind (z.B. das Kraulen und Tragen von Jungtieren). Dies deutet darauf hin, dass OT für die Regulation prosozialer Motivation von besonderer Bedeutung ist.

Ausgehend von den Ergebnissen der ersten Teilstudien habe ich zuletzt untersucht, wie sich spezifische Bindungen und gegenseitiges Kraulen auf die individuelle Beteiligung an der Brutpflege auswirken. Die Ergebnisse zeigen, dass vor allem die Beziehungsqualität zwischen Eltern-Paaren, aber auch zwischen Eltern und Söhnen für deren Beitrag zur Brutpflege ausschlaggebend sind. Kraulen wird dagegen nicht gezielt als „Zahlungsmittel“, z.B. für die Mithilfe bei der Brutpflege oder für den Zugang zu Jungtieren, eingesetzt.

Insgesamt hebt die Arbeit die Schlüsselrolle von OT in der Regulation von sozialen Beziehungen und prosozialem Verhalten in Weissbüschelaffen hervor. Ausserdem betont sie die Bedeutung guter Beziehungen für die individuelle Beteiligung an der Brutpflege und die erfolgreiche Kooperation bei der Jungenaufzucht in Familiengruppen. Im Rahmen eines positiven OT Feedback-Modells diskutiert die Arbeit schliesslich die Möglichkeit einer selbstverstärkenden Regulation von Bindungsverhalten, damit verbundener OT Ausschüttung, und Bindungsstärke. Eine erhöhte OT-Ausschüttung im Zusammenhang mit starken Bindungen und Bindungsverhalten könnte sich zudem auch positiv auf individuelle Prosozialität und Kooperativität innerhalb einer Gruppe auswirken. Die Arbeit leistet einen substantiellen Beitrag zur Aufklärung der proximaten regulatorischen Mechanismen, die der kooperativen Jungenaufzucht in Krallenaffen zugrunde liegen. Damit könnte sie auch helfen, die Sonderstellung menschlicher Kooperativität und Prosozialität im Tierreich besser zu verstehen, da bei Menschen und Krallenaffen eine konvergente Entwicklung von kooperativer Jungenaufzucht und erhöhter Prosozialität vermutet wird.

1. Introduction

1.1. Common marmosets as model species to study prosocial behavior

1.1.1. Marmoset biology and cooperative group-life

Common marmosets belong to the callitrichid monkeys, who are native to Middle and South American rain forests and exhibit a unique lifestyle among primates: They live in relatively small, highly affiliative family groups that are characterized by low levels of within-group aggression and exceptionally high levels of cooperation. Marmoset groups usually consist of a dominant monogamous breeding pair, their dependent offspring, and adult non-reproductive helpers, and most group members are closely related to each other (Rothe et al., 1977). Reproduction is usually limited to one dominant breeding pair, but mating systems and group composition show considerable flexibility, in particular in wild callitrichids, where polyandrous and polygynous breeding also occurs (Garber et al., 2016; Goldizen, 1988; Solomon and French, 1997; Sussman and Garber, 1987). Adult offspring (helpers) often remain philopatric in their natal group for several years and reproductively inactive until their own breeding opportunities become available, e.g. through emigration or inheritance of breeding positions in the natal group (Snowdon and Ziegler, 2007; Tardif, 1997). As a consequence, competition for breeding positions, especially among adult females, occasionally also leads to increased aggression and infanticidal risk in callitrichid groups (Digby, 1995a; Digby et al., 2007).

Cooperation among adult group members in marmosets and other callitrichids primarily concerns joint care for infants, but also includes sharing of resources (food, body warmth) (Brown et al., 2004; Smith et al., 2007), joint foraging (Caine, 1996; Schiel and Huber, 2006), vigilance (Bales et al., 2000; Koenig and Rothe, 1991), and territory and group defense (Garber, 1988; Rylands, 1993; Tardif et al., 1993). The cooperative breeding hypothesis suggests that the coordination of these joint activities is facilitated by higher species-specific socio-cognitive and communicative abilities and emotional/motivational predispositions (other-regarding preferences) towards other group members, including increased social tolerance, attentional biases and responsiveness to others' signals, and spontaneous prosociality towards conspecifics (Burkart et al., 2007 & 2009; Burkart and van Schaik, 2010; Hrdy, 2009; Jaeggi et al., 2010). Available evidence indeed shows that group members in callitrichid monkeys, including

marmosets, monitor each other closely (Snowdon, 2001), and that performances in social learning (Snowdon and Boe, 2003), cooperative problem solving (Cronin and Snowdon, 2008; Snowdon and Cronin, 2007), and gaze understanding (Burkart and Heschl, 2006 & 2007) are particularly high in these species. Unsolicited prosociality has been reported in food provisioning contexts (Burkart et al., 2007; Cronin and Snowdon, 2008; Hauser et al., 2003), and, beyond that, it may also extend to other contexts, such as the sharing of information (Burkart et al., 2009).

1.1.2. Joint care for infants

When infants are born in a marmoset group, breeders - especially mothers - are usually the primary caretakers during the first days post-partum. After that, fathers and adult and sub-adult helpers also contribute substantially to infant-care (Digby et al., 2007; Garber, 1997; Goldizen, 1987b; Yamamoto et al., 2014). It has been shown that the number of helpers is positively related to infant survival and reproductive success, since they reduce the high cost of infant-carrying (Rothe et al., 1993; Santos et al., 1997; Schradin and Anzenberger, 2001; Tardif, 1997). However, not all individuals are always equally involved in caretaking. Potential caretakers may vary in their motivation and willingness to contribute to infant-care, but they may also compete over access to infants, and even highly motivated individuals may not always be allowed to contribute equally (Mills et al., 2004; Yamamoto and Box, 1997; Zahed et al., 2010). Particularly female helpers are often less tolerated by other group members in the presence of young offspring, presumably due to female competition over breeding positions and the associated risk of infanticide (Albuquerque, 1999; Digby, 1995a).

Infant-care during early infancy mostly includes carrying and anogenital licking (Kaplan and Rogers, 1999). As the infants get more independent and start to consume solid food, food provisioning by adult caretakers becomes very important (Ferrari 1987; Feistner and Price 1990, 1991 & 2000; Brown et al. 2004). Especially in the wild, this includes more than simple nutritional supplementation, since the infants also need to learn foraging techniques and to identify edible foods (Rapaport and Brown, 2008; Voelkl et al., 2006). Adult caretakers, including helpers, are thereby very important, as they guide infants actively during the learning process (Rapaport and Brown, 2008), and they even adapt their sharing rates and assistance during food acquisition according to the infants' age and skill level (Martins et al., in preparation; Martins and Burkart, 2013; Rapaport and Brown, 2008).

In my project and collaborative studies with Eloisa Martins, we differentiated and defined food provisioning behaviors following the scheme introduced by Brown et al. (2004): Proactive sharing was initiated by a donor individual, who waited for the recipient (usually infants or immatures) with the food item in his hand or mouth while emitting food calls at the same time, and sharing did not occur in response to begging by the recipient. If the donor shared food in response to begging or after harassment or through stealing, this was recorded as facilitated or resisted sharing, respectively. We recorded sharing rates from adults to immatures up to 63 % of provided food items during peak provisioning periods, and 40 % of these food transfers occurred proactively. Non-reproductive helpers showed particularly high levels of proactive food sharing (48 %) during that time (Finkenwirth et al., 2016; Martins et al., in preparation).

1.1.3. Individual variation in prosocial behavior

The preceding paragraphs have it made clear that marmosets exhibit exceptionally high levels of social tolerance and proactive prosociality, both in naturalistic (Jaeggi and Gurven, 2013; Snowdon and Cronin, 2007) and experimental contexts (Burkart and van Schaik, 2013; Jaeggi et al., 2010). However, individual prosociality also shows considerable variation between groups and individuals, and across an individual's lifetime. Some of this variation may be explained on the group level, e.g. by the presence of infants in a group, group composition, and by sex- and status-specific differences (Burkart, 2015).

The presence of young infants in callitrichid groups is generally associated with higher social tolerance and prosocial performance, which are natural preconditions for infant-directed care-taking behaviors (including infant-carrying, -licking, -grooming, and food sharing) and successful cooperation among adult caretakers. Experimentally assessed food sharing levels, not only towards infants but also among adult group members, increase dramatically (up to 53%) during weeks 10-16 after infant-birth (Martins et al., in preparation; Martins and Burkart, 2013).

Sex and status-specific differences in prosocial performance may be related to different breeding strategies in females and males, which presumably influences the degree and quality of their contribution to infant-care (Yamamoto et al., 2014). Females are dependent on allomaternal helpers to raise their offspring, and compete over breeding positions and helpers in a group. Thus, female helpers often receive more aggression, have a higher risk of eviction from the group, and are less tolerated by dominant females during care-taking than male helpers. This

competition among females is particularly evident in the reproductive inhibition of subordinates, which commonly occurs in female but never in male helpers (Abbott, 1984 & 1993; Barrett et al., 1990).

Callitrichid males tend to be more philopatric (McGrew and McLuckie, 1986) and to rely more on cooperation with male relatives or on the inheritance of breeding-positions in their natal group (Baker et al., 1999; Yamamoto et al., 2014). Especially in the wild, closely related males occasionally even share breeding positions as well as the duties of paternal care-taking, and sons rather seek extra-group copulations than competing with their breeding fathers. Males also seem to be more important during allomaternal infant-care than female helpers, as they carry infants relatively more (Ferrari, 1992; Goldizen, 1987a; Zahed et al., 2010), and the number of male helpers predicts infant survival in wild callitrichid groups better than the number of female helpers or overall group size (Bales et al., 2000; Garber et al., 1984; Koenig, 1995). Furthermore, males show increased levels of care-taking contribution and responsiveness to infant-cues with growing age and experience, whereas female helpers seem to be more ambivalent, starting highly motivated as young caretakers but decreasing their helping contribution with growing age and experience (Barbosa and Da Silva Mota, 2013; Burkart, 2015; Zahed et al., 2010). Burkart (2015) furthermore showed that group levels of proactive prosociality and social tolerance are positively linked to the percentage of male helpers.

Beside these more general patterns, other factors accounting for inter-individual variation in prosociality still remain relatively unexplored. A particular challenge to identify such factors is that helping motivation and cooperative contributions can be expressed in different behaviors that complement each other, i.e. different individuals in a group may show a division of labor rather than contributing with the same behavior to the welfare of the group. Hence, individual prosociality may not be properly assessed by simply comparing all individuals with regard to the same specific behavioral performance. In order to better understand the constraints and flexibility that shape individual prosociality in group-living marmosets, it is thus vital to study the proximate regulation of these behaviors in more detail and to explore new perspectives on the problem. Highly relevant in this context are i) the role of social relationships, that may influence individual cooperativeness, and ii) the hormonal regulation of both social bonding and individual cooperativeness.

1.2. Social bonding and its benefits on cooperation in primates

It is evident from many primate species that high-quality relationships with other conspecifics provide essential fitness benefits for the involved individuals (Kummer, 1978), and that social bonding with specific partners plays an important role in cooperative contexts: Bonding decreases the risk of mortality and increases life span in humans and non-human primates (Holt-Lunstad et al., 2010; Silk et al., 2010). Among female macaques, baboons, and capuchins, bonding and long-term alliance formation positively affect rank orders and reproductive success, including higher infant survival and shorter birth intervals (Kapsalis, 2004; Silk et al., 2003; Silk et al., 2009). Female baboons also benefit from close 'friendship'-like associations with males, since they may provide protection for themselves and their infants (Palombit et al., 1997; Smuts, 1985). Bonding among males is rarer and normally associated with male philopatry and high within-group contest. This is well known from chimpanzees (Mitani, 2009), but has also been described for species with female dispersal such as Assamese macaques (Schülke et al., 2010) and Barbary macaques (Berghänel et al., 2011). The benefits of these bonds include agonistic support, rank changes, and mating privileges, reviewed by Ostner and Schülke (2014) and van Hooff and van Schaik (1994). Evidence from chimpanzees shows that specific bonding is particularly important in cooperative contexts, such as coalitionary support (Mitani et al., 2000; Nishida, 1983; Nishida and Hosaka, 1996), cooperation during hunting (Stanford et al., 1994), food sharing (Boesch and Boesch, 1989), and territory defense (Goodall et al., 1979).

In callitrichid monkeys such as common marmosets, strong long-lasting bonds are formed between mates that show high specific partner preferences and social monogamy (Buchanan-Smith and Jordan, 1992; Carp et al., 2015; Goldizen, 2003). Other dyadic relationships in marmoset groups, e.g. between parents and their adult offspring, who remain in the group, or between adult siblings, are typically also highly affiliative (Schaffner and Caine, 2000). However, it has not been assessed whether these relationships are also differentiated, in that individuals have partners with whom they may preferably interact. If so, the question arises whether cooperation among group-living callitrichids also benefits from partner-specific interactions and bonding. This would be particularly plausible in pair mates, but may also be true for other dyads. Alternatively, the members of a group may simply be equally nice to all others,

without discriminating between specific partners, which would likewise facilitate the task of joint infant-care.

1.3. Monitoring hormonal changes to assess primate relationships

Hormones, especially neurohormones, play an important role in the regulation of social interactions and bonding, e.g. by triggering central reward mechanisms, the activation of emotional responses, or stress attenuation. A special role in the regulation of social behavior of vertebrates is assigned to neuropeptides like oxytocin and vasopressin that act in concert with sex steroids, prolactin, and cortisol. The brain, as their main site of action, is source as well as a target of endocrine functions (Adkins-Regan, 2005; MacDonald, 2010).

Combining behavioral observations and hormonal measures as external and internal perspectives provides a powerful tool to interpret social interactions and to evaluate their relevance for cooperation. For instance, hormonal responses to affiliative or prosocial interactions may show the extent to which individuals react more strongly during interactions with specific partners, i.e. whether group members engage in specific relationships with each other or whether within-group interactions are unspecific and equally reflected in hormonal levels (Crockford et al., 2013). Additionally, prosocial behaviors (e.g. during the joint care for infants) may themselves be linked to hormonal responses on the individual level that can be monitored and interpreted, and this link may provide further information about sex- and status-specific differences in prosocial motivation and performance.

1.4. Oxytocin

The neurohormone oxytocin (OT) is highly relevant for studying social relationships and their influence on cooperation in primates, since it plays a key role in social bonding and in the regulation of affiliative and cooperative interactions among bond partners (see Lim and Young (2006), MacDonald and MacDonald (2010), Marazziti et al. (2006), Olff et al. (2013), and Ross and Young (2009) for extensive reviews). The complex role of OT in mammalian sociality, as observed to date, most likely evolved on the basis of female reproduction and sexual interaction between mates, from where it presumably expanded towards the regulation of maternal care and mother-infant bonding (Kendrick, 2000; Lonstein and Morrell, 2007), bonding between pair

mates and between non-sexual partners (e.g. in ‘friendships’), including affiliative and prosocial interactions as the behavioral basis of social bonding (Broad et al., 2006; Curley and Keverne, 2005; Lim and Young, 2006). Overall, OT is involved in the coordination of behavioral and physiological processes as a central neurotransmitter as well as a peripheral hormone, representing two co-evolved functional pathways (MacDonald, 2010).

1.4.1. Oxytocin origin and receptor system

OT is synthesized in the paraventricular and supraoptic nuclei of the hypothalamus, from where it is projected to the central nervous system or into the posterior pituitary (Heinrichs et al., 2003; Marazziti et al., 2006). The neurohypophysis, as a circumventricular organ, is characterized by an incomplete blood-brain barrier, which allows the direct release of OT into the peripheral circulation, as well as into the brain, even though the carrier mechanisms are not well understood (Balin et al., 1986; Born et al., 2002; Heinrichs et al., 2003; Parker et al., 2005). OT is furthermore also synthesized in variable peripheral tissues including the uterus, placenta, amnion, corpus luteum, testis, and the heart (Burbach et al., 2006; Gimpl and Fahrenholz, 2001).

The two-part OT-receptor-hormone system of vertebrates generally refers to the local OT concentration and the alteration in receptor density and location. Beside their location in peripheral tissues, OT-receptors are found in a variety of socially relevant and stress-sensitive limbic brain regions (Gimpl and Fahrenholz, 2001). They are expressed sex-specifically under the influence of the gonadal steroid hormones estrogen and testosterone. Carter (2003) drew a link between early receptor synthesis in the postnatal period and resulting lifelong consequences on social behavior (pair bonding and parenting) in adult voles, since OT receptor distributions can vary strongly between individuals according to rearing experiences and social environment (Feldman et al., 2010; Fries et al., 2005; Winslow et al., 2003).

1.4.2. Oxytocin effects

OT effects in mammals have been most intensely studied in the context of female reproduction, including the stimulation of the mammary glands and milk letdown during lactation (Kendrick and Keverne, 1989; Uvnäs-Moberg et al., 2001), and the initiation of uterine contraction and labor (Blanks and Thornton, 2003; Kendrick and Keverne, 1989; Landgraf et al.,

1983; Nissen et al., 1995). Moreover, OT is important for mother-offspring bonding and the regulation of maternal behavior (Insel, 1990; Uvnäs-Moberg, 1996), which has been shown in mice (Ross and Young, 2009), rats (Pedersen et al., 1994), sheep (Kendrick et al., 1987), and humans (Levine et al., 2007).

In sexual contexts, OT also plays a role in the regulation of socio-sexual behavior and pair bonding (Carmichael et al., 1987; Kendrick et al., 1987; Sansone et al., 2002). This has been shown in prairie voles (Bales et al., 2007; Williams et al., 1994) and callitrichids, where experimental manipulation facilitated partner preference and fidelity among mates (Cavanaugh et al., 2014; Smith et al., 2010; Snowdon et al., 2010), and urinary OT levels correlate with a mate's socio-sexual behavior (Snowdon et al., 2010). Furthermore, in humans, OT receptor variability is associated with behavioral traits reflecting pair-bonding (Walum et al., 2012).

Affiliative and cooperative interactions are essential components of social bonding, especially in non-sexual contexts, and a broad body of evidence suggests that OT is important for the regulation of affiliative and cooperative behaviors in mammals (Lim and Young, 2006): In chimpanzees, where long-term bonds with specific partners are particularly important (Mitani, 2009), grooming (Crockford et al., 2013) and food sharing (Wittig et al., 2014) among two partners elicits increased OT responses, but only when strongly bonded partners are involved. More unspecific, partner-independent positive effects were reported from experimental studies in rats (Ramos et al., 2013), naked mole rats (Mooney et al., 2014), and meerkats (Madden and Clutton-Brock, 2011), where peripheral OT treatment facilitates prosocial affiliation, and communal cooperative activities (digging, guarding, infant-care). Furthermore, intranasal and intracerebral OT administration promotes food sharing in marmosets (Saito and Nakamura, 2011a) and social donation behavior in rhesus macaques (Chang et al., 2012). However, inhibitory effects on food sharing have also been reported for marmosets (Mustoe et al., 2015), where intranasal OT administration reduces prosocial sharing toward strangers, and in capuchin monkeys (Brosnan et al., 2015), where OT leads to decreased sharing due to increased social distance. Investigating partner-specific OT effects is still a relatively new endeavor, independent of the usage of endogenous levels or exogenous OT manipulation. Thus, some OT effects reported above may need to be re-tested and re-evaluated with regard to potential partner-specific effects.

Evidence from humans and non-human primates shows that OT is also directly involved in social cognition, especially in prosocial and cooperative contexts in normal healthy subjects. For example, OT enhances social memory (Dantzer et al., 1987; Guastella et al., 2008b), social attention (gaze to faces) (Guastella et al., 2008a), social recognition (reviewed in Guastella and MacLeod, 2012), and empathic emotional response (Shamay-Tsoory et al., 2013) in humans, and it increases prosocial choices in an experimental setting in macaques (Chang et al., 2012). Furthermore, intranasal OT administration and endogenous OT levels are positively linked to prosocial perception and trust (Bartz et al., 2011; Baumgartner et al., 2008; Domes et al., 2007; Kosfeld et al., 2005; Zak et al., 2004). Such positive effects presumably also involve the activation of neural reward circuits via specific OT receptor activation in the respective brain areas (Insel, 2010).

Another important function of OT in social and non-social contexts is the buffering against stress (Heinrichs et al., 2009; Olff et al., 2013), including lowered cortisol levels, reduced blood pressure (Woodbury et al., 1944), and increased wound-healing (Detillion et al., 2004). This has been shown experimentally in mice (Ring et al., 2006) and humans (Radke et al., 2013). Acute anxiolytic and stress-reducing effects are probably also socially mediated (Heinrichs et al., 2003) and triggered by affiliative interactions (Seltzer et al., 2010).

1.4.3. Monitoring urinary oxytocin to assess social dynamics in marmosets

Monitoring peripheral OT levels via urine is advantageous in behavioral studies, since it allows the repeated, non-invasive sampling of endogenous OT levels related to repeated social interactions. This is especially valuable for the non-invasive monitoring of natural dynamics of social interactions and relationships in wild and semi-wild living animals, such as marmoset groups. In contrast, conventional methods that require direct handling and invasive sampling of blood, saliva, or cerebrospinal fluid are very stressful for the animals and exclude the possibility of repeated sampling and continuous monitoring, especially in natural environments. Furthermore, these methods bear the risk of confounding stress-related OT effects, since the oxytocinergic system also interacts with the stress axis.

Contradictory results in animal and human studies and a rapidly growing usage of exogenous OT in experimental contexts, however, have given rise to an ongoing debate on the coordination between central and peripheral OT levels and the study of peripheral OT levels

related to central effects (Guastella and MacLeod, 2012). Several clearance studies support a correlation between systemic and urinary OT changes (Amico et al., 1987; Mitsui et al., 2011; Seltzer and Ziegler, 2007). Experimental evidence from rats (Wotjak et al., 1998) and humans (Carson et al., 2014), as well as correlated activity in concomitant axonal projections to brain and pituitary in rats and voles (Knobloch et al., 2012; Ross et al., 2009a; Ross et al., 2009b) also suggest a coordination of central and peripheral OT release. A link or coordination between central and peripheral domains is furthermore indicated by the finding that exogenous OT administration leads to a correlated OT increase in brain and plasma, e.g. in rats, following intranasal and peripheral OT administration (Neumann et al., 2013), and in macaques, following peripheral OT injection (Freeman et al., 2016). In contrast, studies in goats (Seckl and Lightman, 1987), pig-tail macaques (Rosenblum et al., 2002), and lactating rhesus monkeys (Amico et al., 1990) indicate that central and peripheral levels are controlled independently. However, whether the release of central and peripheral OT is coordinated also seems to depend on OT-receptor distributions (Gimpl and Fahrenholz, 2001) and the stimulating brain regions involved (e.g. in the paraventricular nucleus) (Martínez-Lorenzana et al., 2008), and is most likely indirectly influenced by other hormones such as steroids (Bos et al., 2012; McCarthy, 1995; Ochedalski et al., 2007). Overall, this suggests that the oxytocinergic system needs to be considered a functional whole, including central and peripheral sites of action and OT release that may occupy partly different functional areas but are not acting completely independently. Furthermore, a coordination between central and peripheral domains seems to be highly dependent on the nature and context of a specific OT effect, e.g. with regard to reproduction-related processes versus social interactions and bonding.

A broad body of experimental evidence suggests a positive link between peripheral OT levels and positive social interactions in mammals: Peripheral OT administration was found to exert stimulating effects on affiliation towards same-sex conspecifics in rats (Ramos et al., 2013) and on communal cooperative activities (digging, guarding, pup-feeding, and associating with pups) in meerkats (Madden and Clutton-Brock, 2011). In turn, endogenous peripheral OT levels in plasma and urine are associated with positive social interactions, emotional states, and socio-cognitive processes: Plasma OT levels increase in response to affiliative interactions in rats (Stock and Uvnäs-Moberg, 1988), and elevated urinary OT levels are associated with grooming (Crockford et al., 2013) and food sharing (Wittig et al., 2014) in chimpanzees, with visual and

physical contact in marmosets (Seltzer and Ziegler, 2007), and with affiliation and socio-sexual contact in tamarins (Snowdon et al., 2010) and macaques (Moscovice and Ziegler, 2012). In humans, plasma and urinary OT also increases in response to positive physical contact (Morhenn et al., 2008), parent-infant affiliation (Feldman et al., 2011), hearing social vocalizations (Seltzer et al., 2010), receiving social support (Holt-Lunstad et al., 2008), and performing paternal behavior (Gordon et al., 2010b). Short-term social distress is also associated with elevated OT levels (Feldman et al., 2011; Taylor et al., 2010), whereas long-term depressive states in women are reflected in lowered longitudinal plasma OT levels (Cyranowski et al., 2008). Interestingly, urinary OT levels even reflect positive interactions between species, e.g. between humans and dogs, where urinary OT levels increase in the human dog owners after they engaged in visual contact with their dogs (Nagasawa et al., 2009), and in dogs after they received stroking from their owners (Mitsui et al., 2011). Altogether, this evidence shows that peripheral OT levels are useful to study positive interactions in very different social contexts.

Urinary OT levels seem to be particularly advantageous since they provide a direct window into acute as well as long-term OT responses to social interactions and social environmental stimuli (Crockford et al., 2014). The findings of Crockford et al. (2013) and Wittig et al. (2014) in chimpanzees even suggest that urinary OT responses to affiliative and prosocial interactions reflect partner-specificity, in that OT levels are only elevated after interactions with strong-bond partners. Hence, based on the available evidence in humans and non-human primates, monitoring urinary OT levels may provide a useful tool for the monitoring of social interactions and for evaluating the valence of specific relationships in marmoset family groups.

In the studies that are part of this thesis, I exclusively detected OT from morning void urine. Compared to short-term OT fluctuations in plasma and saliva, urinary OT concentrations result from the accumulated excretion of systemic OT over several hours and even overnight, assuming that sleep is not interrupted with social contact or urination. Especially morning urine thus rather reflects average OT values that result from the sum of all affiliative interactions during the hours before sleep, and that are presumably also influenced by other factors, such as an individual's reproductive status or prosocial motivational state. In combination with behavioral data, this sampling method allows for assessing the link between OT levels and individual affiliative and prosocial behaviors, and for looking at the integration of social

interactions with different partners at the hormonal level over time. The methods of urine sampling and OT detection are described in detail as part of the first thesis chapter.

1.5. Thesis objectives and study parts

The overall aim of my PhD thesis was to broaden the existing knowledge on the role of the neurohormone oxytocin (OT) in the regulation of social group life and cooperation, and how this may explain individual variation in prosocial behaviors, in group-living common marmosets. Specifically, I investigated the relationship structure of marmoset family groups based on individual longitudinal OT patterns and behavioral data, and how OT is linked to individual cooperativeness during infant-care. Furthermore, I aimed to tie these effects together by assessing the influence of dyadic relationships on individual care-taking contribution.

My thesis is structured into four main chapters that explore OT patterns underlying the structure of marmoset dyadic relationships (chapter 2), the stability of such patterns and relationships over time (chapter 3), the link between OT and individual infant-care behavior and motivation (chapter 4), and the influence of dyadic relationships on individual infant-care behavior (chapter 5).

1.5.1. Oxytocin and dyadic relationships in marmoset family groups (chapter 2)

In the first empirical study of this thesis, I investigated urinary OT patterns underlying the dyadic relationship structure in marmoset family groups. Specifically, I tested whether individual OT levels were related to dyadic affiliative interactions, and whether this link was dyad-specific, in that affiliative interactions among strongly bonded individuals affect OT levels more than interactions with other individuals. Whereas marmoset breeding pairs are known to engage in long-lasting, socially monogamous bonds, it is unknown whether partner-preferences also occur between other group members. First, this should be indicated by increased partner-specific affiliation among bonded partners, which is arguably easier to assess in non-reproductive periods, when individuals are not preoccupied with infant-care. Over time, bonded partners were expected to show synchronized longitudinal OT levels, since affiliative interactions among chimpanzees elicit partner-specific OT responses in urine, and strongly bonded partners should thus also influence each other's OT levels more than non-bonded

partners in marmoset groups. The results of this chapter show that stronger bonded marmoset dyads have synchronized OT levels, independent of the dyad type. This suggests that OT responses to affiliative interactions are partner-specific, thus reflecting differentiated relationships among group-living marmoset breeders and helpers.

1.5.2. Assessing the stability of marmoset relationships over time (chapter 3)

The second study investigated whether the dyadic relationships, identified in chapter 2, are stable over time, possibly fulfilling an adaptive function, e.g. with regard to cooperative infant-care. If so, patterns of dyadic affiliation and OT synchrony as well as the degree to which an individual was integrated in its group (the sum of its affiliative interactions with all other group members) should be consistent between two different periods, in particular in periods when dependent offspring are present. To test this, I used the existing data on dyadic affiliation, dyadic OT synchrony, and individual group integration from chapter 2 and compared them with values that were collected six months later in a period when reproductive offspring were present in the same groups. I found that patterns of dyadic affiliation and OT synchrony as well as individual group integration were consistent between the non-reproductive and the reproductive study period, which indicates that differentiated relationships among group-living marmosets are stable for at least six months.

1.5.3. Oxytocin and care-taking behavior in marmoset family groups (chapter 4)

In the third study, I assessed the role of OT in infant-care behavior and motivation of adult marmoset caretakers. OT positively regulates maternal care and mother-infant bonding in mammals, and some evidence suggests that it may also be involved in allomaternal care. Marmosets are a key species to study this question, since they show extensive allomaternal care by fathers and non-reproductive helpers. Here, I tested whether individual urinary OT levels of adult marmoset group members increase after infant-birth, and whether OT is linked to care-taking behaviors (infant-carrying, -licking, -grooming, and proactive food sharing) during three postpartum months. I thereby considered that behaviors involving more physical contact with infants (e.g. carrying and grooming) may show different OT effects than proactive food sharing, which is particularly suitable to assess intrinsic care-taking motivation, because food can be

shared by all caretakers with infants ad libitum, whereas physical access to infants and carrying may be restricted to few individuals. Since the regulation of care-taking behavior may significantly involve motivational stimulation, it is crucial to make this differentiation with regard to potential related OT effects. I found that all adult marmoset caretakers show increased OT levels directly after the birth of a new set of infants, and that individual OT levels are positively linked to infant-licking during early infancy and to proactive food sharing during late infancy, whereas no effect was found for infant-grooming or -carrying. This suggests that OT is particularly involved in behaviors that reflect care-motivation, and that these effects correspond to the changing needs of growing infants over time.

1.5.4. Consequences of relationship quality on individual cooperativeness (chapter 5)

The aim of the last study was to integrate the findings from the previous chapters, and to investigate how affiliative interactions and dyadic relationships among group-living marmosets influence individual contribution to infant-care. Evidence from different primate species suggests that strong bonds facilitate cooperation in the involved individuals. Single individuals may even use directed grooming towards specific recipients to strengthen the relationship with a potentially helpful partner or to pay the partner for help or access to infants. With regard to cooperative infant-care in marmoset groups, both scenarios are possible, but their specific effects on individual care-taking contribution have not been tested so far. Here, I investigated whether breeders use grooming to pay helpers for infant-care or whether helpers use grooming to pay breeders for access to infants, or, alternatively, whether care-taking contribution in breeders and helpers is generally rather determined by the quality of their relationship with other group members. The results of this chapter show that both breeder females and males contributed more to infant-care, when they received more grooming from their partner before birth, whereas no such effect was found among breeders and helpers. Furthermore, care-taking contribution was positively linked to dyadic relationship quality in breeding pairs and mother-son dyads. Hence, these findings suggest that mutual relationship quality rather than strategically directed grooming is relevant for subsequent individual care-taking and, thus, successful cooperation in marmoset family groups.

2. Strongly bonded family members in common marmosets show synchronized fluctuations in oxytocin

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2.1. Abstract

Oxytocin is a key regulator of social bonding and is positively linked to affiliation and prosocial behavior in several mammal species. In chimpanzees, this link is dyad-specific as affiliative interactions only elicit high oxytocin release if they involve strongly bonded individuals. These studies involved isolated dyads and sampling events. Little is known about the role of oxytocin in affiliation and social bonding, and about potential long-term patterns of bonding-related and dyad-specific oxytocin effects within highly affiliative and cooperative social groups. Our aim was to investigate whether bonding-related oxytocin signatures linked to dyadic affiliation are present in family groups of cooperatively breeding marmoset monkeys (*Callithrix jacchus*) that show high levels of cohesion and cooperation. In 30 dyads from four family groups and one pair, we measured urinary baseline oxytocin over six weeks and analyzed the link to bond strength (mean dyadic affiliation). Strongly bonded dyads showed synchronized longitudinal fluctuations of oxytocin, indicating that dyad-specific oxytocin effects can also be traced in the group context and in an interdependent species. We discuss these results in light of the potential function of differentiated relationships between marmoset dyads other than the breeding pair, and the role of oxytocin as mediator for social bonding.

2.2. Introduction

The neurohormone oxytocin (OT) plays an important role in the regulation of mammalian social bonds and bonding related behaviors (Feldman et al., 2011; Fries et al., 2005; Kendrick, 2000; Kendrick et al., 1987; Seltzer et al., 2010; Williams et al., 1994; Witt et al., 1990). Its functions presumably have been expanded from the more ancient mother-infant and sexual bonds to a wider range of relationships in highly social species, including primates (Broad et al., 2006; Curley and Keverne, 2005). A broad body of evidence suggests a positive link between OT and affiliative or prosocial interactions, as for example in rats (Ramos et al., 2013), meerkats (Madden and Clutton-Brock, 2011), and humans (Zak et al., 2004). In the latter, elevated peripheral OT levels correspond with increased trust, and intranasal OT administration facilitates social perception and trust (Bartz et al., 2011; Baumgartner et al., 2008; Domes et al., 2007; Kosfeld et al., 2005).

In non-human primates, OT correlates have been mainly studied in callitrichid monkeys and chimpanzees. Increased urinary OT concentrations accompany socio-sexual and affiliative interactions in both species (Crockford et al., 2013; Snowdon et al., 2010) and food sharing events in chimpanzees (Wittig et al., 2014). The results in chimpanzees have shown that such effects can be dyad-specific, in that increased urinary OT levels were detected only after affiliative interactions between socially bonded individuals, but not between non-bonded individuals (Crockford et al., 2013; Wittig et al., 2014). Individuals in chimpanzee societies form strong and long-lasting social bonds that are thought to entail direct and indirect fitness benefits (Langergraber et al., 2009; Mitani, 2009), and OT responses related to specific group members have been suggested to facilitate non-cognitive bookkeeping of social relationships (Crockford et al., 2013).

The bonding-dependent release of OT during affiliative interactions is also consistent with experimental results. Intranasal and intracerebral OT administration affects partner preference (Cavanaugh et al., 2014; Smith et al., 2010) and paternal food transfer in marmosets (Saito and Nakamura, 2011a). The experimental increase in OT thus mimics the effect of affiliative interactions with bonded individuals. As a result, subjects treat the experimental partners like stronger bonded individuals. The effects of OT application in humans can also be interpreted this way (Bartz et al., 2011; Baumgartner et al., 2008; Domes et al., 2007; Kosfeld et al., 2005).

Crockford et al. (2013) showed that OT secretion following dyadic affiliation is higher in strongly bonded dyads compared to interactions in less bonded dyads. Consequently, an individual's OT profile should be particularly determined by its affiliative events with strongly bonded group members, whereas interactions with other group members should influence its OT profile less. Over time, this should lead to temporal correlations in the OT profiles of bonded dyads, i.e. synchronized peaks and troughs of baseline OT, reflecting how much the bonded individuals are engaging in affiliative behavior with each other. No such tendency toward synchronized changes over time should occur in non-bonded dyads, because affiliative interactions in such dyads is expected to have no or a much smaller effect on OT. The aim of our study was to investigate the degree of dyadic OT synchrony in family groups of cooperatively breeding marmoset monkeys, in which affiliative interactions are frequent among all group members and some individuals form strong dyadic relationships (Evans and Poole, 1984; Schaffner and Caine, 2000). Marmoset groups are typically composed of a dominant breeding pair, several adult helpers, and immatures (Hubrecht, 1984; Rothe et al., 1977). Relationships between breeding pairs involve intense partner-directed affiliative and sexual behavior (Anzenberger and Falk, 2012; Evans, 1983; Evans and Poole, 1984; Schaffner and Caine, 2000; Snowdon et al., 2010), and are characterized as socially monogamous (Digby, 1995a; Epple, 1977; Evans, 1983; Ferrari and Digby, 1996; Ferrari and Lopes Ferrari, 1989; Rothe, 1975; Savage et al., 1988; Schaffner et al., 1995). The relationships between other group members are mostly peaceful and cooperative (Schaffner and Caine, 2000), even though punctual events of severe aggressions occur, in particular related to competition for breeding positions (Digby et al., 2006).

Specifically, we investigated the link between urinary baseline OT and dyadic affiliation in family groups of common marmosets (*Callithrix jacchus*) in order to test whether dyad-dependent OT response patterns are traceable within the family environment in this species, and whether temporal changes in baseline OT are synchronized in dyads, depending on their bond strength. If so, OT synchronization was expected to be most pronounced in stronger bonded marmoset dyads (estimated based on mean dyadic affiliation). This should especially apply to breeding pairs where specific monogamous bonds are accompanied by high levels of affiliation and socio-sexual behavior (Evans, 1983; Evans and Poole, 1984), but it may also occur in non-

breeding individuals, whose relationships with other group members have barely been studied so far.

Urinary OT levels provide a proxy for peripheral OT, and have the advantage that they can be repeatedly sampled noninvasively, and thus without interrupting the social dynamics within the groups through invasive handling. The relevance of peripheral OT measures for studying the dynamics of social relationships has been recently reviewed and discussed by Crockford et al. (2014). OT is synthesized in various peripheral organs as well as in the hypothalamus, from where it is released peripherally and centrally (Goodson and Thompson, 2010; Lim and Young, 2006). Several studies suggest a direct link (Ayers et al., 2011; Madden and Clutton-Brock, 2011; O'Byrne et al., 1990; Witt et al., 1990) as well as coordination between both systems based on neuroanatomical and physiological evidence (Carter et al., 2007; Ross and Young, 2009; Wotjak et al., 1998). This link is probably also triggered indirectly, for example via steroid hormones (Bos et al., 2012; McCarthy, 1995; Ochedalski et al., 2007) and bidirectional feedback mechanisms with peripheral organs and body states (Goodson and Thompson, 2010), but the topic remains debated (Feldman et al., 2011; Veening et al., 2010). Whereas cerebrospinal fluid (CSF) and plasma OT levels are positively correlated in humans (Carson et al., 2014), no such link was found in goats (Seckl and Lightman, 1987), pig-tail macaques (Rosenblum et al., 2002), and lactating rhesus monkeys (Amico et al., 1990), suggesting independent control mechanisms of central and peripheral OT secretion. However, whether the release of central and peripheral OT is coordinated, seems to also depend on the involved stimulating brain regions (e.g. in the paraventricular nucleus) (Martínez-Lorenzana et al., 2008). This indicates high flexibility and context-dependent activation of central and peripheral OT pathways. Several clearance studies support a correlation between systemic and urinary OT changes (Amico et al., 1987; Mitsui et al., 2011; Seltzer and Ziegler, 2007). In various species, including humans and non-human primates, both plasma and urinary OT levels have been found to correspond with social environmental stimuli (Crockford et al., 2013; Feldman et al., 2011; Fries et al., 2005; Mitsui et al., 2011; Moscovice and Ziegler, 2012; Nagasawa et al., 2009; Seltzer and Ziegler, 2007; Seltzer et al., 2010; Snowdon et al., 2010; Wittig et al., 2014) or physiological and psychological states (Cyranowski et al., 2008; Mitchell et al., 1982; Moscovice and Ziegler, 2012; Tops et al., 2007). In contrast to short-term OT fluctuations in plasma and saliva, urinary OT concentrations, especially detected from the first

morning void, result from the net effect of accumulation and excretion of systemic OT over several hours. Morning urine should thus also be relevant for monitoring baseline OT levels as the summed excretion of elevated OT responses related to dyadic affiliative behavior (Crockford et al., 2014) in callitrichid monkeys. In combination with behavioral data, this sampling method allows looking at the integration of social interactions with different partners at the hormonal level over time.

2.3. Methods

2.3.1. Subjects and housing

The study was performed using four common marmoset family groups (N = 3 to 5 individuals) and one male-female pair, amounting to a total of 19 adult individuals (9 females and 10 males, supplementary table S 2.1), aged between 2.3 to 9.5 years. No dependent offspring (nursing and being carried) were present at any time during the study. All groups were housed in standardized enclosures (depending on group size, one or multiple basic cage units; each measuring 2.4 m height x 1.5 m depth x 0.8 m width, with max. 3 animals per cage unit) at the Primate Station of the Anthropological Institute and Museum, University of Zurich. Each enclosure had a spacious outdoor area (measuring 2.4 m height x 2.7 m depth x 2.5 m width) and was equipped with a sleeping box, a water dispenser, several wooden climbing structures, an infrared lamp, and a mulch floor. The animals were housed under natural light with additional artificial light on a 12 h/12 h light–dark cycle and UV light (300W). Their diet consisted of a vitamin and calcium-enriched porridge in the morning, fresh fruits and vegetables over midday, as well as gum and mealworms in the afternoon, and water was available ad libitum. A special cage unit for urine collection was attached to each home cage and only accessible in the morning during urine collection (Anzenberger and Gossweiler, 1993). On urine sampling days, mealworms were fed in the urine cages in the morning instead of afternoon.

2.3.2. Urine sampling and OT analysis

For OT detection, morning urine samples of all 19 individuals were collected two to three times a week (alternating groups between 2 and 3 sampling days per week) over six consecutive

weeks (total n = 275 samples). The sampling was restricted to morning void urine, in order to measure hormonal baseline values and to minimize confounding effects of circadian rhythms. This was done non-invasively either in a urine cage or with a plastic cup in the home cage, as described elsewhere (Anzenberger and Gossweiler, 1993). Urine cages were made of transparent plastic panels and separated into six compartments with individual trap doors and access to a feeding trough at the backside. A wire-mesh and a metal panel with drains and adjustable vessels under each compartment allowed the collection of individual samples without contamination. Before the sampling period, animals were habituated over several weeks to enter and feed in the cage voluntarily. After awakening the group in the morning, animals were allowed to access the urine cage and kept in separate compartments until after urinating, but no longer than 15 minutes in total. The urine cages were rinsed carefully after each usage. Urine samples were labelled right after collection and stored immediately at -20°C in 1 ml portions until analysis.

OT was detected using ELISA technique in the Assay Services Unit of the Wisconsin National Primate Research Center in Madison, Wisconsin, according to the protocol by Seltzer and Ziegler (2007) and Snowdon et al. (2010). Urine samples were run in duplicates at a volume of 200 µl. Prior to OT detection, samples were thawed, centrifuged, and extracted using solid phase extraction columns (Macherey-Nagel, 55–150 mm, WAT023501). Extraction columns were conditioned with 1 ml 100% methanol and 1 ml purified water. Samples were added (0.5 ml urine), washed with 1 ml 10% acetonitrile, 1% TFA (trifluoroacetic acid) in water, and eluted with 1 ml 80% acetonitrile in water. Samples were dried, reconstituted in 250 µl assay buffer, and added to the microtiter plates according to the directions provided with the assay kit (Assay Designs, Cat no. 901-153). The assay standard curve ranged from 6 to 1000 pg/ml and assay sensitivity was 6 pg/ml. Mean intra-assay coefficients of variation and inter-assay coefficients of variation were 5.85 % and 16.11 %, respectively. All OT concentrations were corrected for creatinine levels to control for variable urine concentration and log-transformed (log pg OT/mg Cr) to reach normal distribution prior to statistical analysis (Kolmogorov-Smirnov test for normality: $D(275) = 0.037$, $p = 0.33$).

2.3.3. Behavioral observations and analysis

In order to investigate the link between bond strength and OT synchrony, marmoset groups were observed for affiliative behavior along with the urine sampling over six weeks. We

observed the groups 2-3 times per week on alternating days and recorded all social interactions based on continuous sampling in 10-minute focal observations for each individual within its group. Affiliative behaviors, including allogrooming (defined as using hand and/or mouth to pick through fur, face or mouth of another individual) and huddling (defined as sitting or lying in body contact with another individual), were used to estimate bond strength (the average over all dyadic affiliative events). Agonistic behavior was very rare and therefore not included in the analysis. All observations were performed by the same observer using an established protocol (see also Koski and Burkart (2015); a test for inter-observer reliability with an independent observer resulted in 0.89 percent of agreement). An average of 173 ± 3.48 observation minutes were available for each individual. Urine samples were always collected the next morning, following observation days.

2.3.4. Statistical data analysis

Dyadic bond strength was estimated based on dyadic affiliation - mean rates of mutual grooming and huddling - for all 30 dyads, i.e. 5 breeder-breeder (mates), 18 breeder-helper (parent-adult offspring) and 7 helper-helper (siblings) dyads (supplementary table S 2.2). Durations of affiliative behaviors were corrected for observation time and combined into one log-transformed value (log[sec grooming + sec huddling]/sec observed). Dyadic OT synchrony was calculated as the Pearson correlation coefficient of the longitudinal OT fluctuations of two partners (N = 8 to 13 OT values per dyad), resulting in one synchrony value per dyad (table S 2.2).

First, we analyzed variation of individual urinary OT levels between sex-status groups (female and male breeders and helpers) and variation of dyadic bond strength (mean dyadic affiliation) between breeder-breeder, breeder-helper and helper-helper dyads, using analysis of variance (R: one-way ANOVA; completely randomized design). Post-hoc tests between groups and effect sizes for ANOVA results were calculated using Scheffe-test and eta square, respectively.

Second, we tested whether strongly bonded dyads showed higher OT synchrony and whether this relationship was affected by dyad type, using a permutation-based linear model (R version 3.0.3: lmPerm, Exact permutation analysis). The permutation step was included (i) to compensate for small sample size, and (ii) to control for dependencies due to individuals

participating in multiple dyads in a group, by randomly resampling dyadic OT synchrony and affiliation values across groups. Dyadic OT synchrony was the dependent variable and dyadic bond strength, dyad type, and the interaction dyadic bond strength*dyad type were included as factors.

2.4. Results

Mean individual baseline OT levels (mean ± SE) of female breeders, male breeders, female helpers, and male helpers were 2.99 ± 0.24, 2.85 ± 0.26, 2.53 ± 0.16, and 2.74 ± 0.25 (log pg OT/mg Crt), respectively. Differences between sex-status groups were non-significant (one-way ANOVA: $F(3, 15) = 0.84$, $P = 0.49$, $h^2 = 0.14$), but OT levels tended to be highest in female breeders.

Dyadic bond strength (rates of mutual dyadic affiliation) varied widely across all dyad types. Mean ± SE values for breeder-breeder, breeder-helper and helper-helper dyads were 0.087 ± 0.016, 0.026 ± 0.004 and 0.017 ± 0.006 (log sec/sec observed), respectively, and dyadic bond strength was significantly higher in breeder dyads than in the two other dyad types (one-way ANOVA and post-hoc Scheffe: $F(2, 27) = 18.43$; $P < 0.001$, $h^2 = 0.58$) (figure 2.1).

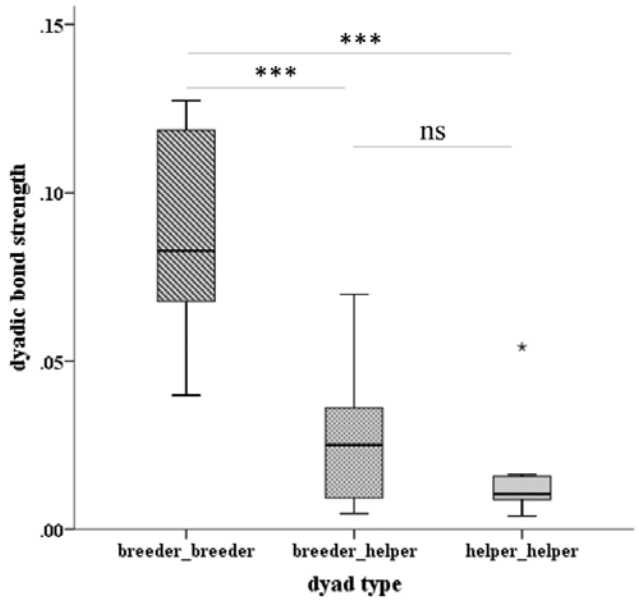

Figure 2.1: Bond strength in different dyad types. Variation in mean dyadic levels of affiliation (dyadic bond strength) in 5 breeder-breeder, 18 breeder-helper, and 7 helper-helper

dyads. Mean dyadic affiliation is significantly higher in breeder-breeder dyads compared to the other dyad types.

Dyadic OT synchrony values, calculated as Pearson correlation coefficient for each dyad, varied between r = -0.55 and 0.82 with 5 significant correlations (16.6 % of the total 30 dyads). The permutation ANOVA on dyadic OT synchrony revealed an effect of dyadic bond strength (mean dyadic affiliation), and dyad type, whereas the interaction dyadic bond strength*dyad type had no effect (table 2.1). Figure 2.2 illustrates longitudinal OT levels and OT synchrony of two strongly (2.2A) and two weakly (2.2B) bonded individuals. The link between dyadic bond strength and OT synchrony was significant across all dyad types (table 2.1, Linear model estimate = 10.14, $P < 0.01$). It was equally strong in breeder-breeder and helper-helper dyads, but weaker in mixed breeder-helper dyads, where variation was broader (figure 2.3).

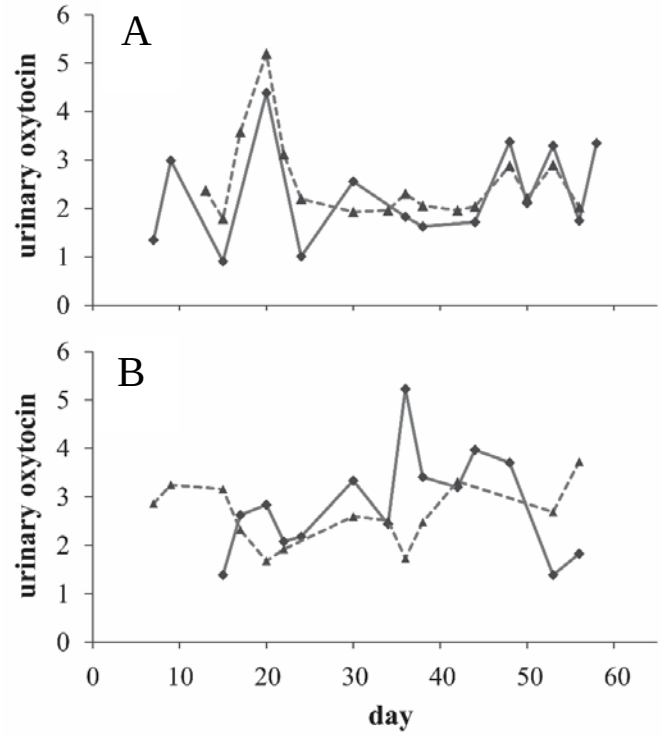

Figure 2.2: Temporal correlation of urinary OT in two dyads. OT levels (log pg OT/mg Crt) in a strongly bonded (A) and a weakly bonded (B) dyad; both dyads are composed of a female breeder (solid lines) and a male helper (dashed lines). Dyadic OT synchrony values for A and B are 0.79 and -0.41, respectively.

Figure 2.3 shows the relationship between dyadic OT synchrony and dyadic bond strength. The right shift of the regression line in breeder-breeder dyads (solid red regression line) compared to other dyads reflects the relatively higher levels of dyadic affiliation in breeders. However, this shift did not affect the significant link between OT and bond strength across dyad types, as indicated by the non-significant interaction between dyadic bond strength and dyad type (table 2.1). The residual distribution of the linear model was normal (Shapiro-Wilk normality test: W = 0.97, P = 0.46), suggesting a good model fit to the data.

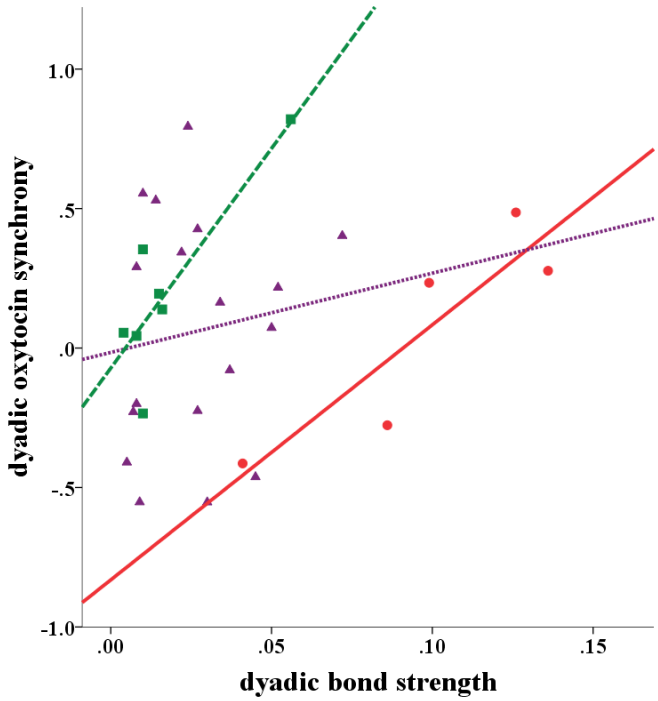

Figure 2.3: Positive link between dyadic bond strength and OT synchrony. The pattern shows a similarly strong trend for breeder-breeder (dots, solid red line; R^2 Linear = 0.582) as well as helper-helper dyads (squares, dashed green line; R^2 Linear = 0.713), but a weaker trend for mixed breeder-helper dyads (triangles, dotted purple line; R^2 Linear = 0.170).

Table 2.1: Permutation-based linear model results table. Analysis of the influence of dyadic bond strength (mean dyadic affiliation) and dyad type on dyadic OT synchrony in group-living marmoset dyads. Dyad type levels are coded as BB (breeder-breeder), BH (breeder-helper), and HH (helper-helper). Parameter estimates: factor levels with bars are compared with remaining factor levels. Bold: $p < 0.05$.

model factor	F	df	p-value	factor level	estimate	p
dyadic bond strength	**9.84**	**1**	**0.004**		**10.14**	**0.004**
dyad type	**2.90**	**2**	**0.075**	**BH**	**-0.39**	**0.024**
				HH	0.03	0.361
				BB	-	-
dyadic bond strength*dyad type	0.89	2	0.424	BH	-2.90	0.322
				HH	-4.24	0.286
				BB	-	-

2.5. Discussion

In this study, we explored whether dyadic bond strength in group-living marmoset monkeys was linked to synchronized fluctuations in longitudinal OT levels. We found that strongly bonded dyads exhibit synchronized fluctuations of urinary baseline OT over time, both in breeder-breeder dyads and other dyad types. These findings are consistent with the dyad-specificity of OT responses to affiliative behavior in chimpanzees (Crockford et al., 2013), because they suggest that an individual's OT profile is particularly determined by its affiliative interactions with strongly bonded group members, whereas interactions with other group members influence its OT profile less. Over time, this arguably leads to the reported temporal correlations and synchronization of OT profiles in bonded dyads, reflecting how much the individuals engaged in affiliative behavior with each other. Furthermore, the findings suggest the existence of differentiated dyadic relationships in marmosets, which is consistent with the species' characteristic stable and long-lasting relationships between mate pairs (Schaffner and Caine, 2000). However, strongly bonded dyads with synchronized OT fluctuations were not exclusively found among breeding pairs, as the pattern also extended to breeder-helper and helper-helper dyads.

The relationships between callitrichid group members other than the breeding pair are mainly shaped by their cooperatively breeding lifestyle (Snowdon and Cronin, 2007), but the function of differentiated relationships as described here remains to be established. Stronger relationships between same-sex helpers may provide benefits during dispersal (Monteiro da Cruz, 1998), whereas close breeder-helper relationships may result in increased future

allomaternal care by helpers (in particular if breeders are more responsible for establishing and maintaining these relationships) or in longer periods of acceptance in the natal group (in particular if helpers are more responsible for establishing and maintaining these relationships). Alternatively, differentiated relationships between group members other than breeding pairs might simply reflect the extent to which an older individual was engaged in caring for a younger individual during infancy (Kostan and Snowdon, 2002), or finally occur as a by-product of the mechanism that has evolved in this species to maintain stable and long lasting socially monogamous relationships between mates. Aggressive interaction were too rare to include them in our evaluation of dyadic relationships. However, earlier studies have shown that breeding competition among females, leading to severe aggression and occasional infanticide, is part of callitrichid group life, especially in the wild (Digby and Saltzman, 2009; French and Inglett, 1989; Yamamoto et al., 2014; Yamamoto et al., 2009), and may thus also play a role in shaping dyadic relationships.

The link between dyadic OT synchrony and bond strength (affiliation) was found to be positive across all dyad types but it was strongest in breeder-breeder and helper-helper dyads, and, in breeder dyads, the correlation was relatively shifted to the right (figure 2.3). This pattern shift originated from the significantly higher levels of dyadic affiliation in breeders compared to other dyads, which are probably partly resulting from breeding pairs spending more time in proximity during periods of increased sexual activity during the female ovarian cycle (Stevenson and Poole, 1976). Whether our dyadic proximity estimates for breeding pairs are comparable to those in more heterogeneous groups or in the wild, where the turn-over for breeding positions is also faster (Lazaro-Perea et al., 2000), remains unknown. Compared to breeder-breeder and helper-helper dyads, the link between OT synchrony and affiliation was weaker in mixed breeder-helper dyads, possibly because breeder-helper relationships are more heterogeneous (Yamamoto et al., 2014). Importantly, we can rule out high relatedness as a factor driving OT levels or OT synchrony. All members of a group, except the breeding pairs, were directly related and our pattern does not indicate better synchronization between siblings (including twins) or parent-offspring dyads than between mates (figure 2.3).

A potential error source of variation in the observed link between synchronized longitudinal OT fluctuations and dyadic affiliation is sexual cycling in reproductively active females, since estrogen is known to have a stimulatory effect on OT (McCarthy, 1995;

Ochedalski et al., 2007). This mainly pertains to breeding females but may also include subordinate female helpers. Sexual cycling in subordinate females is usually inhibited (Abbott, 1984; Barrett et al., 1990) but reproductive suppression occasionally fails in daughters after they reach puberty (Abbott, 1984; Digby, 1995a; Ziegler and Sousa, 2002). However, removing all dyads that contain breeding females from the data set does not erase the significant effect of dyadic bond strength in the linear model analysis (Linear model estimate=10.99, p=0.02).

The pattern of dyadic synchronization as presented in our data is consistent with studies on marmoset dyadic behavioral synchrony (Melo et al., 2013) and on human parent-infant bonding: Human infants, whose fathers had been previously treated with exogenous OT, showed an indirect increase of peripheral OT levels after interaction with the father (Feldman et al., 2011; Weisman et al., 2012) and longitudinal synchronization between individuals occurred on the behavioral level (Feldman, 2007; Feldman, 2012; Feldman et al., 2011). Finally, in humans, menstrual hormonal synchrony has been described among close friends and in families where mutual contact and exposure were high (Weller et al., 1995; Weller et al., 1999). These analogous patterns suggest that temporal coordination between individuals can occur on the behavioral as well as on the physiological level and might hence represent a more general functional mechanism in social bonding.

2.6. Conclusion and implications

Our results show that, in common marmosets who live in family groups, more strongly bonded dyads have more synchronized longitudinal fluctuations of urinary baseline OT levels compared to less strongly bonded dyads. This patterning indicates that, despite the high cohesiveness among marmoset groups, OT responses are to some extent dyad-specific. Our results are thus consistent with the positive link between dyadic affiliative behavior and elevated urinary OT in strongly bonded chimpanzees, and with a possible role of OT as a mediator of social interactions and bonding, as suggested by Crockford et al. (2013) and Wittig et al. (2014). Between-individual OT effects may thereby be established and maintained via positive feedback mechanisms triggered by affiliative (Crockford et al., 2013), but also gaze (Nagasawa et al., 2009; Nagasawa et al., 2015) or voice (Seltzer et al., 2010) interactions. Intriguingly, highly affiliative dyads with synchronized OT fluctuations were not exclusively found among breeding pairs, but also among breeder-helper and helper-helper dyads. The presence of differentiated

relationships among non-breeding dyads raises the question about the ultimate function of such relationships.

Finally, hormonal synchronization between two individuals may represent a hitherto neglected dimension in the establishment and maintenance of social relationships. It remains to be established in future studies whether such shared longitudinal fluctuations of OT also lead close individuals to share mood shifts and whether such a connection could provide a hormonal link to psychological and emotional consequences of bonding.

2.7. Acknowledgements

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2.8. Supplementary material

Table S 2.2.: Individual information. Individual group membership, name, sex, status, and age of all 19 individuals that were part of this study.

group	individual	sex	status	age
Kapo	Kapo	male	breeder	9.09
Kapo	Marlene	female	breeder	3.50
Marilyn	Marilyn	female	breeder	9.46
Marilyn	Monroe	male	breeder	8.61
Marilyn	Marlon	male	helper	3.50
Mina	Mina	female	breeder	5.23
Mina	John	male	breeder	4.56
Mina	Mibba	female	helper	2.29
Mina	Membo	male	helper	2.29
Nina	Nina	female	breeder	5.22
Nina	Lex	male	breeder	5.22
Nina	Nigg	male	helper	2.70
Nina	Nari	male	helper	2.70
Nina	Nala	female	helper	2.26
Lancia	Lancia	female	breeder	9.10
Lancia	Lexus	male	breeder	8.21
Lancia	Lea	female	helper	4.13
Lancia	Larissa	female	helper	3.46
Lancia	Leon	male	helper	3.46

Table S 2.3. Dyadic information. Dyad-specific group membership, composition, OT synchrony, and affiliation values for all 30 dyads that were part of this study.

group	group size (N ind)	dyad nr	individual 1	individual 2	dyad type	dyadic OT synchrony	dyadic affiliation
Kapo	2	1	Kapo	Marlene	breeder_breeder	0.23	0.068
Marilyn	3	2	Marilyn	Monroe	breeder_breeder	0.49	0.119
Marilyn	3	3	Marilyn	Marlon	breeder_helper	0.34	0.022
Marilyn	3	4	Monroe	Marlon	breeder_helper	0.07	0.049
Mina	4	5	Mina	John	breeder_breeder	0.28	0.127
Mina	4	6	Mina	Mibba	breeder_helper	0.53	0.014
Mina	4	7	Mina	Membo	breeder_helper	0.79	0.024
Mina	4	8	John	Mibba	breeder_helper	0.29	0.008
Mina	4	9	John	Membo	breeder_helper	0.55	0.010
Mina	4	10	Mibba	Membo	helper_helper	0.82	0.054
Nina	5	11	Nina	Lex	breeder_breeder	-0.41	0.040
Nina	5	12	Nina	Nigg	breeder_helper	-0.41	0.005
Nina	5	13	Nina	Nari	breeder_helper	-0.55	0.009
Nina	5	14	Nina	Nala	breeder_helper	-0.08	0.036
Nina	5	15	Lex	Nigg	breeder_helper	-0.23	0.007
Nina	5	16	Lex	Nari	breeder_helper	0.43	0.026
Nina	5	17	Lex	Nala	breeder_helper	-0.46	0.044
Nina	5	18	Nigg	Nari	helper_helper	0.14	0.016
Nina	5	19	Nigg	Nala	helper_helper	0.06	0.004
Nina	5	20	Nari	Nala	helper_helper	0.35	0.010
Lancia	5	21	Lancia	Lexus	breeder_breeder	-0.28	0.083
Lancia	5	22	Lancia	Lea	breeder_helper	-0.23	0.027
Lancia	5	23	Lancia	Larissa	breeder_helper	0.40	0.070
Lancia	5	24	Lancia	Leon	breeder_helper	0.16	0.034
Lancia	5	25	Lexus	Lea	breeder_helper	0.22	0.051
Lancia	5	26	Lexus	Larissa	breeder_helper	-0.55	0.030
Lancia	5	27	Lexus	Leon	breeder_helper	-0.20	0.008
Lancia	5	28	Lea	Larissa	helper_helper	0.04	0.008
Lancia	5	29	Lea	Leon	helper_helper	0.20	0.015
Lancia	5	30	Larissa	Leon	helper_helper	-0.24	0.010

3. Long-term-stability of relationship structure in family groups of common marmosets

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Submitted to: Physiology and Behavior

3.1. Abstract

Recent results suggest differentiated relationships in cooperatively breeding, group-living common marmosets, reflected in partner-specific affiliative interactions and dyadic oxytocin synchrony (OTS) among strong-bond partners during a period of six weeks. Intriguingly, strong relationships do not only occur between breeding partners but between individuals from any sex or status. To date, it is unclear whether such relationships are stable over time and fulfill an adaptive function, e.g. with regard to cooperative infant-care, or whether they are short-lived, transient phenomena. To assess the long-term stability of the relationship structure of common marmoset family groups, we investigated whether hormonal and behavioral measures of group structure (dyadic OTS, dyadic affiliation, and individual group integration) in common marmoset families remained stable over a period of six months. We collected baseline urinary OT and social behavior of 36 dyads from three family groups in a non-reproductive period (period A), and again six months later, around the birth of new infants (period B). Patterns of dyadic OTS, dyadic affiliation, and individual group integration were consistent between the two study periods. These results suggest that differentiated relationships are stable for at least six months, even between group members other than the breeding pair. Future studies are necessary to identify whether these relationships have an adaptive function, perhaps with regard to potentially positive consequences on cooperativeness.

3.2. Introduction

Cooperatively breeding callitrichid monkeys like common marmosets live in relatively small and cohesive family groups, in which breeding and non-breeding group members cooperatively care for dependent offspring. This lifestyle and the joint care for infants are associated with high within-group affiliation, and increased social tolerance and prosocial motivation towards other group members (Burkart et al., 2014; Garber, 1997; Schaffner and Caine, 2000), even though episodes of intense conflict also occur, in particular when competing for breeding positions (Digby et al., 2007).

Marmoset families are typically composed of parents (breeders), adult offspring, and non-adult offspring (Koenig and Rothe, 1991). Breeders are socially most central, as they are the most frequent grooming partners (Digby, 1995b) and in closer proximity to most other group members, compared to adult offspring who often occupy more peripheral positions (Koenig and Rothe, 1991). The relationships of breeding pairs are relatively well studied and described as socially monogamous (Goldizen, 2003; Snowdon and Ziegler, 2007; but see Díaz-Muñoz and Bales, 2016; Garber et al., 2016), whereas less is known about the relationship structure among other group members in marmoset family groups. It has been shown that callitrichid breeders generally groom their offspring more than vice versa, suggesting that breeders may specifically use grooming as incentive for helpers to stay in the group (Ginther and Snowdon, 2009; Lazaro-Perea et al., 2004; Löttker et al., 2007). However, recent evidence also suggests that grooming patterns in marmosets are more dyad-specific and that individuals have preferred grooming partners in their group (Finkenwirth et al., 2015). Intriguingly, more affiliative partners also show synchronized fluctuations of urinary oxytocin (OT) levels over time, suggesting that OT responses are particularly influenced by affiliative interactions with their most important grooming partners (Finkenwirth et al., 2015).

OT is involved in early mother-infant bonding (Uvnäs-Moberg, 1996) and in the formation of pair-bonds between sexual partners in many mammal species (Lim and Young, 2006). Together with previous findings in chimpanzees (Crockford et al., 2013; Wittig et al., 2014) our results (Finkenwirth et al., 2015) suggest that OT also plays a role in non-sexual relationships of group-living primates. Bond strength and the intensity of OT responses related to affiliative interactions with specific partners are thereby thought to be mediated in a positive feedback loop. Consequently, affiliative interactions among stronger bonded partners

presumably lead to higher OT release than interactions in non-bonded partners. Such partner-specific OT patterns can be detected directly in response to affiliative events (Crockford et al., 2013) or indirectly as longitudinal dyadic OT synchrony (OTS) in strong-bond partners (Finkenwirth et al., 2015). Together, the available evidence indicates that marmoset group members engage in differentiated dyadic relationships, regardless of the composition of the dyad, at least during a period of six weeks.

The function and consequences of differentiated relationships suggest that they are of adaptive value in many primate species. In particular, reliable bonds among primates have been associated with increased fitness and health (reviewed in Kummer, 1978; Silk, 2007a; Silk et al., 2010), e.g. in pigtail macaques (Boccia et al., 1989) and baboons (Silk et al., 2010), with increased post-conflict reconciliation in pigtail macaques and chimpanzees (Castles et al., 1996; de Waal, 1986), with higher social rank and the possibility of rank changes due to coalitionary support (reviewed in Ostner and Schülke, 2014; van Hooff and van Schaik, 1994), e.g. in chimpanzees (Fraser et al., 2008; Nishida and Hosaka, 1996) and macaques (Massen, 2010), and with increased cooperation in chimpanzees, e.g. during hunting (Stanford et al., 1994), food sharing (Boesch and Boesch, 1989), and territory defense (Goodall et al., 1979). Indirectly this is associated with higher reproductive success, e.g. in female baboons (Lemasson et al., 2008; Palombit et al., 1997; Silk et al., 2009) and women (Collins et al., 1993), and in male macaques (Schülke et al., 2010), chimpanzees (Gilby et al., 2013), and baboons (NOË and Sluijter, 1990).

In group-living marmosets, reliable bonds may be particularly valuable in the context of cooperation during the joint care for infants. Joint care-taking involves complex coordination of infant-transfers and carry-shifts (taking turns during infant-carrying) between caretakers, and it requires increased tolerance among caretakers in the proximity of young infants. If so, the relationship structure of the group, detected during a period without dependent offspring, should remain stable during reproductive periods, when dependent offspring are present in the group. Relationships between breeders and helpers may also result in longer periods of acceptance of the helpers in the natal group, or increased allomaternal care by helpers (chapter 5, Finkenwirth and Burkart, in preparation-a; Snowdon and Cronin, 2007). Strong bonds between same-sex helpers may furthermore provide benefits during dispersal (Garber et al., 2016; Monteiro da Cruz, 1998). In all three cases, differentiated relationships as described in Finkenwirth et al.

(2015), and thus group structure, are predicted to be stable over time rather than a short-lived transient phenomenon.

The aim of this study was to investigate the stability of relationship structures in family groups of common marmosets. We studied three marmoset groups (14 individuals) and compared their relationship structure during a non-reproductive period (period A, 6 weeks per group, see Finkenwirth et al., 2015) with a second period B, six months later, around the birth of new infants (6 to 12 weeks, starting one week pre-partum). In one group, two litters of infants were born, resulting in a total of four litters included in the study. In both periods, we measured longitudinal urinary OT levels to assess dyadic OTS as hormonal proxy of relationship quality, and conducted focal observations of all social behaviors with other group members to assess dyadic affiliation and individual group integration, i.e. the sum of all dyadic affiliation that an individual shared with other group members. We tested the stability of dyadic OTS, dyadic affiliation, and individual group integration over time. Based on the assumption that strong bonds are functional, perhaps because they facilitate cooperation in infant-care, result in longer periods of acceptance of the helpers in the natal group, or may provide benefits during dispersal, we predicted patterns of dyadic OTS, dyadic affiliation, and individual group integration to be correlated between study parts A and B.

3.3. Methods

3.3.1. Study animals

We studied three marmoset family groups (14 individuals) in a non-reproductive period (part A) and in a reproductive period (part B), where dependent offspring were present. In part B, one group (Nina) was sampled twice over two reproductive cycles. Individual group membership, name, sex, and status of all adult marmosets that were part of this study, as well as the order and date of sampling events in study period A and B are listed in supplementary tables S 3.3-A and B.

The groups were housed in standardized enclosures (depending on group size, one or multiple basic cage units; each measuring 2.4 m height x 1.5 m depth x 0.8 m width), that were connected to spacious outdoor areas and equipped with a sleeping box, a water dispenser, several wooden climbing structures, an infrared lamp and a mulch floor. Indoor enclosures provided

natural light and additional artificial light on a 12 h/12 h light–dark cycle and UV light (300W). The animals received a vitamin and calcium-enriched porridge in the morning, fresh fruits and vegetables over midday, as well as gum and mealworms in the afternoon. Water was always available ad libitum. Each enclosure was connected to a special cage unit that was only accessible in the morning during urine collection. On urine sampling days, mealworms were fed as reward in the urine cages in the morning instead of afternoon (see Finkenwirth et al., 2015 for details).

3.3.2. Urinary oxytocin detection

We collected baseline morning urine samples for the detection of individual OT levels two to three times per week during each sampling period over six weeks in part A and over six to 12 weeks in part B, starting one week prior to birth. OT levels from study period A and B were measured using ELISA technique in the Assay Services Unit of the Wisconsin National Primate Research Center in Madison, Wisconsin, and the endocrinology laboratory of the department of Primatology at the Max Planck Institute of Evolutionary Anthropology, Leipzig, Germany, respectively. The urine sampling and OT detection procedures are described in detail in (Finkenwirth et al., 2015 & 2016). After collection, urine samples were immediately stored in 1 ml aliquots at -20°C until measurement. For OT detection, samples were thawed, vortexed, and extracted using solid phase extraction columns (Macherey-Nagel, 55–150 mm, WAT023501). Extracted urine samples were measured in duplicates at a volume of 200 µl according to the directions provided with the assay kit (Assay Designs, Cat no. 901-153). Dyadic OTS was calculated as the correlation coefficient of two individuals' longitudinal urinary OT levels (Finkenwirth et al., 2015) for all within-group dyads in each sampling period. The question whether peripheral OT levels are meaningful estimators of central OT effects related to social behavior and bonding has extensively been discussed in detail in Crockford et al. (2013 & 2014) und Finkenwirth et al. (2015 & 2016).

3.3.3. Behavioral observations

Behavioral observations in period A and B were conducted 2-3 times per week on alternating days. We recorded all social interactions, including mutual grooming (picking the fur

or skin of a partner with hands or mouth) and huddling (resting in direct body contact). Agonistic behavior was too rare to be included in the analysis. In period A, behaviors were recorded as all occurrences based on continuous observations for 10 minutes per individual (40 to 60 minutes per group), whereas in period B, we scanned all individuals in a group every 5 minutes over 120 minutes (24 scans per observation day and group). Urine samples were always collected the next morning, following observation days. All observed behaviors were corrected for observation time or the number of scans, respectively. Furthermore, all affiliation measures were z-transformed prior to analyses in order to eliminate potential variation emanating from the different recording methods. For each dyad, mutual grooming and huddling was combined into one value of dyadic affiliation by summing up the observed frequencies of both behaviors prior to z-transformation. Individual group integration was calculated as the sum of all dyadic affiliation values that an individual shared with other group members.

3.3.4. Statistical data analysis

To assess the stability of dyadic OTS and dyadic affiliation, we used permutation-based linear model analyses (R version 3.0.3: lmPerm, Exact permutation analysis) to control for pseudoreplication, as described in Finkenwirth et al. (2015). A permutation step was included in the linear models to control for dependencies due to individuals participating repeatedly or in multiple dyads in a group, by randomly resampling dyadic OT synchrony in period A and B across groups. By doing so, we controlled for pseudo-replication across periods and across the different reproductive cycles. The best-fitting models were selected based on the Akaike information criterion (AIC) estimation. Approximate normality and homogeneity of residuals was assessed visually based on residuals plotted against fitted values and qq-plots. All model assumptions were met.

First, we tested whether dyadic OTS from period A (OTS-A) was related to OTS from period B (OTS-B) (model 1). OTS-B was the dependent variable, and OTS-A and dyad type were included as fixed factors. Second, we tested whether dyadic affiliation from period A (affiliation A) was related to affiliation from period B (affiliation B) (model 2). Dyadic affiliation B was the dependent variable, and dyadic affiliation A, dyad type, and the interaction dyadic affiliation A*dyad type were included as fixed factors.

To assess the stability of individual group integration from period A to period B (model 3), we used linear mixed-effect model analysis with restricted maximum likelihood estimation (R version 3.1.0, lme package). Individual group integration from part B was the dependent variable, whereas group integration from part A, sex, and status were included as fixed factors, and individual nested in family group was used as random factor.

3.4. Results

3.4.1. Dyadic OTS and affiliation over time

Assessing the stability of OTS values over time revealed a positive link between OTS from periods A and B, with a positive influence of dyad type, emanating from breeder-helper dyads (table 3.1, model 1). The link between OTS from periods A and B was strongest and significant in breeder-helper dyads (Rho=0.54*, p=0.010, N=22), followed by helper-helper (Rho=0.34, p=0.333, N=10) and breeder-breeder dyads (Spearman's Rho=0.32, p=0.684, N=4) (figure 3.1a). However note that the sample sizes for breeder-breeder and helper-helper dyads are very small to assess the effect independently.

Assessing the stability of dyadic affiliation over time, we found a highly significant link between dyadic affiliation values from periods A and B (table 3.1, model 2). Furthermore, we found a negative effect of dyad type, emanating from helper-helper dyads, and an interaction between dyad type and affiliation during period A. These effects show that breeders had higher levels of dyadic affiliation than other dyad types (Figure 3.1b). Furthermore, they indicate that levels of dyadic affiliation decrease among helpers in period B relative to period A, which may reflect that relatively more affiliation was exchanged in the context of infant-care in part B, especially in those dyads that included the main caretakers – namely breeders and some male helpers.

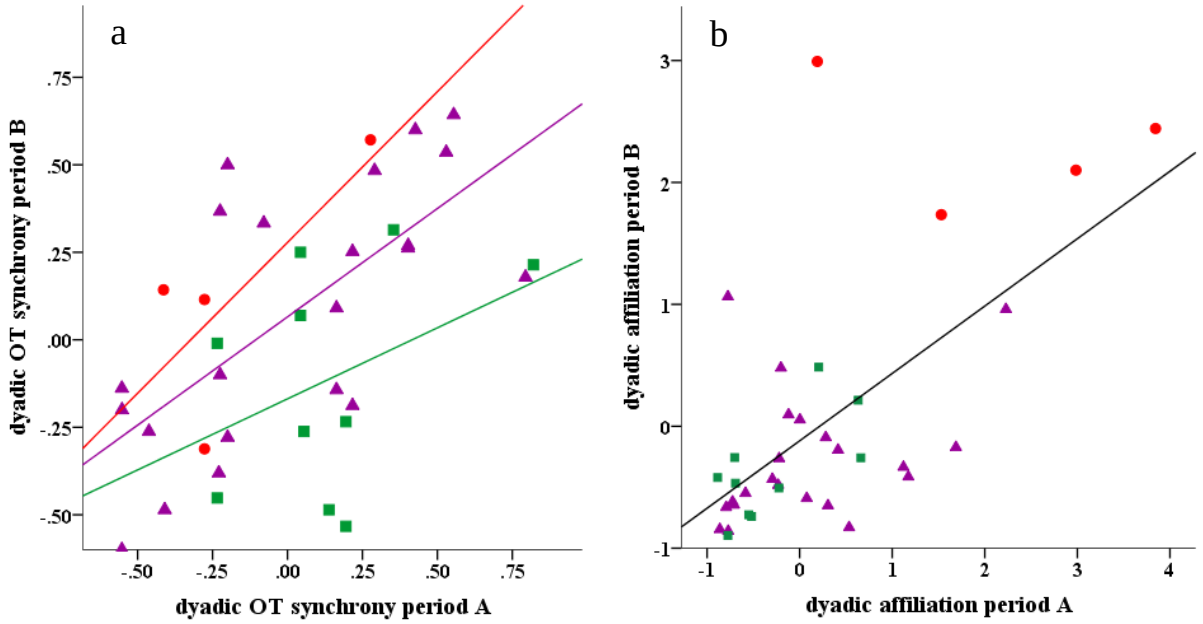

Figure 3.1: Stability of dyadic OT synchrony and dyadic affiliation over time. Dyadic OT synchrony (a) and dyadic affiliation (b) are stable between study parts A and B across breeder-breeder (red circles), breeder-helper (purple triangles), and helper-helper dyads (green squares).

Table 3.1: Permutation-based linear model results table. Analysis of the link between dyadic OTS from part A and B (model 1) and dyadic affiliation from part A and B (model 2). Dyad type coding: BB (breeder-breeder), BH (breeder-helper), and HH (helper-helper) was included as fixed factor. Factor levels with bars are compared with remaining factor levels. Bold: $p < 0.05$.

Model	Dependent variable	Model factor	F	df	p-Value	Factor level	Estimate	p
1	**OTS B**	**OTS A**	**6.46**	**1**	**0.01**		**0.54**	**0.014**
		dyad type	2.15	2	0.13	**BH**	**0.22**	**0.041**
						HH	-0.04	0.823
						BB	-	-
2	**affiliation B**	**affiliation A**	**5.87**	**1**	**0.022**		**0.50**	**0.023**
		dyad type	**3.48**	**2**	**0.044**	BH	0.77	0.270
						HH	**-0.77**	**0.011**
						BB	-	-
		affiliation A*dyad type	**3.32**	**2**	**0.049**	**affiliation A*BH**	**-0.47**	**0.047**
						affiliation A*HH	-0.43	0.098
						affiliation A*BB	0	0

3.4.2. Individual group integration over time

Individual group integration was consistent between study periods A and B, as shown in figure 3.2 and indicated by the positive effect of group integration A on group integration B in model 3 (table 3.2). Sex or status had no effect in this model, which indicates a similar effect direction in all status-sex groups. This finding suggests that, despite significant social changes (the birth of new offspring), individuals do not only maintain their dyadic relationships but also their relative social integration (characterized by the sum of their total affiliative interactions) in the group.

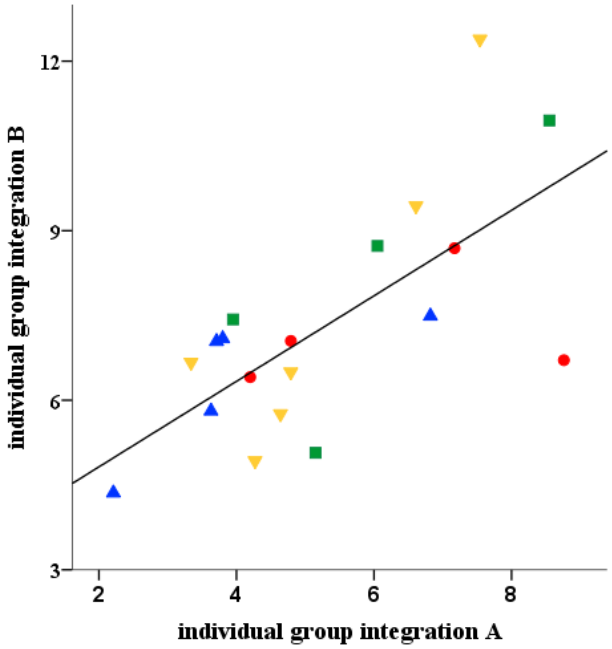

Figure 3.2: Stability of individual group integration over time. Group integration is stable between study periods A and B across breeder females (red circles), breeder males (green squares), helper females (orange triangles), and helper males (blue triangles).

Table 3.2. **Linear mixed-model results table.** Analysis of the link between individual group integration from periods A (integration A) and B (integration B). Status and sex were included as fixed factors and individual nested in family as random factor. Parameter estimates: factor levels with bars are compared with remaining factor levels. Bold: $p < 0.05$.

dependent variable	model	model factor	F	df	p-Value	factor level	estimate	t-value	p
integration B	3	**integration A**	**9.35**	**1**	**0.038**		**0.80**	**3.04**	**0.039**
		status	0.54	1	0.482	helper	0.59	0.73	0.482
						breeder	-	-	-
		sex	0.14	1	0.719	male	0.34	0.47	0.648
						female	-	-	-

3.5. Discussion

In this study, we investigated whether hormonal and behavioral indicators of differentiated dyadic relationships in group-living marmosets remain stable between a non-reproductive and a reproductive sampling period, separated by six months. We found that patterns of dyadic OTS and affiliation, as well as individual group integration (individual sum of total affiliation with other group members) were consistent between these two distinct study periods.

The stability of dyadic affiliation was influenced by dyad type, reflecting the higher affiliation values in breeding pairs, dyadic affiliation tended to be lower when infants were present ($t(35)=-1.40$, $p=0.171$). This pattern presumably reflects time-budget trade-offs during the presence of infants, i.e. that partners from strongly bonded dyads were less likely to interact with each other, probably because the preferred partners were engaged in infant-care and thus not always available. However, dyadic OTS patterns showed no such trend ($t(35)=-0.67$, $p=0.507$) and they were in fact highly stable over the two periods. Individual group integration increased for all individuals ($t(18)=5.76$, $p<0.001$), indicating that overall, more affiliative behavior was exchanged among all group members when infants were present. This indicates that group cohesion generally increases when infants are present, even though intensified affiliative interactions may not primarily be exchanged between preferred partners but rather in the context of joint infant-care. Together, our findings indicate that marmosets engage in stable differentiated relationships with other group members, since individuals do not only seem to keep their preferred bonding partners but also their relative social position (affiliativeness with other group members) and structural integrity in a group. Furthermore, they show that at the same time, group cohesion increases when infants are present in the group.

Our findings are corroborated by a similar effect in a completely unrelated dataset that was collected from a fourth marmoset family group during two periods in a different study context. The group contained six adult individuals (ten dyads) and was housed in the same colony at the Primate station Zurich, and no dependent offspring were present during both sampling periods. Urinary OT values from these additional samples were detected with a different OT assay (supplementary table S 3.4) and were therefore not included in the present study. Nonetheless, combining these additional data with the dataset of the present study strengthened the overall link between dyadic OTS values from two different time periods (supplementary table S 3.4, Linear model estimate=0.63, p=0.014). The fact that dyadic OTS values were stable in both datasets, with a strong positive effect over all data, suggests that dyadic OTS patterns are indeed a reliable estimator of differentiated dyadic relationships in group-living marmosets, and that structural stability is not an artefact in either of the datasets.

A potential source of variation in peripheral OT measurements in the present study may be inherent in reproduction-related OT functions, especially with regard to parturition and lactation in breeding females (Blanks and Thornton, 2003; Uvnäs-Moberg et al., 2001), and may be related to infant-directed behaviors during care-taking. After the birth of infants, absolute OT levels increase in all group members in common marmoset families, and some variation in OT is directly linked to care-taking activities, in particular infant-licking and food sharing (Finkenwirth et al. 2016). Nonetheless, our results show that the stability of dyadic OTS patterns over time is not disturbed by the birth of infants in period B. This indicates that despite the presence of infants and engagement in care-taking, partner-specific OT responses persist and continue to reflect dyadic partner preferences.

The stability of relationships and group structure in marmosets, at least up to six months, is consistent with the idea that these relationships are functional. Maintaining a strong relationship, independently of significant changes in the social environment, may allow partners to cooperate more easily and to be more efficient in the coordination of infant-transfers and -carrying. This may be particularly relevant for breeding pairs and dyads including breeder females and helpers, since breeding females need to breastfeed infants regularly, and this needs to be coordinated smoothly with other caretakers. Aggression and competition about infant-possession would be particularly obstructive for this coordinated action. Thus, future studies need to investigate whether differentiated relationships and high individual group integration are

indeed conducive for cooperativeness in marmoset groups, and potentially other cooperatively breeding species. If so, the question arises whether bonding and group integration are simply beneficial because they facilitate coordination and cooperation among partners, or whether they are actually associated with higher care-taking motivations and commitment on the individual level. Such effects would be particularly expected for those dyads that are primarily important during infant-care (breeder-breeder and breeder-helper dyads). Our recent work in progress focusses on these questions (chapter 5, Finkenwirth and Burkart, in preparation-a).

3.6. Acknowledgements

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3.7. Supplementary material

Table S 3.3-A: Individual information. Individual group membership, name, sex, status of all 14 individuals that were part of this study.

group	individual	sex	status
Lancia	Lancia	female	breeder
Lancia	Lexus	male	breeder
Lancia	Lea	female	helper
Lancia	Larissa	female	helper
Lancia	Leon	male	helper
Mina	Mina	female	breeder
Mina	John	male	breeder
Mina	Mibba	female	helper
Mina	Membo	male	helper
Nina	Nina	female	breeder
Nina	Lex	male	breeder
Nina	Nigg	male	helper
Nina	Nari	male	helper
Nina	Nala	female	helper

Table S 3.3-B: Sampling order. Order and pairing of sampling events from period A (no offspring present) and B (dependent offspring present). To compare data from sampling events 6 (allocated to period A) and 7 (period B) despite the presence of infants in event 6, behavioral and hormonal data from event 6 were restricted to the late postpartum period (week 5-11). The stability of dyadic OT synchrony and affiliation between sampling periods A and B was analyzed over the total sum of 36 dyads.

Sampling events		Sampling period		group	Number of:	
A	B	A	B		Individuals	dyads
1	4	Oct - Nov 2011	June - July 2012	Lancia	5	10
2	5	Oct - Nov 2011	June - July 2012	Mina	4	6
3	6	Oct - Nov 2011	June - July 2012	Nina	5	10
6	7	June - July 2012	Dec 2012 - Jan 2013	Nina	5	10

Table S 3.4: Permutation-based linear model results table. Analysis of the link between dyadic OTS from two distinct sampling periods based on the data sampled for this study as well as an additional data set from a marmoset family group with 8 individuals that was not part of this study. Oxytocin values of the two data sets were measured with different ELISA assays that

were validated independently. Dyad type with the coding BB (breeder-breeder), BH (breeder-helper), and HH (helper-helper) was included as fixed factor. Parameter estimates: factor levels with bars are compared with remaining factor levels. Bold: $p < 0.05$.

Dependent variable	Model factor	F	df	p-Value	Factor level	Estimate	p
OTS B	**OTS A**	**9.21**	**1**	**0.004**		**0.63**	**0.014**
	dyad type	1.61	2	0.210	BH	0.19	0.435
					HH	-0.05	0.534
					BB	-	-

4. Oxytocin is associated with infant-care behavior and motivation in cooperatively breeding marmoset monkeys

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4.1. Abstract

The neurohormone oxytocin (OT) is positively involved in the regulation of parenting and social bonding in mammals, and may thus also be important for the mediation of alloparental care. In cooperatively breeding marmosets, infants are raised in teamwork by parents and adult and sub-adult non-reproductive helpers (usually older siblings). Despite high intrinsic motivation, which may be mediated by hormonal priming, not all individuals are always equally able to contribute to infant-care due to competition among caretakers. Among the various care-taking behaviors, proactive food sharing may reflect motivational levels best, since it can be performed ad libitum by several individuals even if competition among surplus caretakers constrains access to infants. Our aim was to study the link between urinary OT levels and caretaking behaviors in group-living marmosets, while taking affiliation with other adults and infant age into account. Over eight reproductive cycles, 26 individuals were monitored for urinary baseline OT, care-taking behaviors (baby-licking, -grooming, -carrying, and proactive food sharing), and adult-directed affiliation. Mean OT levels were generally highest in female breeders and OT increased significantly in all individuals after birth. During early infancy, high urinary OT levels were associated with increased infant-licking but low levels of adult-affiliation, and during late infancy, with increased proactive food sharing. Our results show that in marmoset parents and alloparents, OT is positively involved in the regulation of care-taking,

thereby reflecting the changing needs during infant development. This particularly included behaviors that are more likely to reflect intrinsic care motivation, suggesting a positive link between OT and motivational regulation of infant-care.

4.2. Introduction

Over the last decades, oxytocin (OT) has been shown to be versatilely involved in the regulation of mammalian social behaviors and bonding (Lim and Young, 2006), most importantly in maternal care and mother-infant bonds (Kendrick, 2000; Uvnäs-Moberg, 1996). Its ancient functions in female reproduction, related to cervix and uterus distension during labor (Blanks and Thornton, 2003; Kendrick and Keverne, 1989; Landgraf et al., 1983; Nissen et al., 1995), milk injection during lactation (Uvnäs-Moberg et al., 2001), and the regulation of maternal behavior (Feldman, 2007; Kendrick, 2000; Kendrick et al., 1987; Pedersen et al., 1994; Uvnäs-Moberg, 1996), probably formed the basis for derived OT functions in non-maternal social contexts (Broad et al., 2006; Kendrick, 2000; Lim and Young, 2006). However, less is known about the role of OT in alloparental care, i.e. care provided by non-mothers, including paternal care provided by fathers.

Among nonhuman primates, alloparental care is most frequent in the cooperatively breeding callitrichid monkeys (Digby et al., 2007). Whereas all group members cooperate in rearing offspring, reproduction is usually restricted to a dominant breeding pair (Digby et al., 2007; Garber, 1997; Goldizen, 2003), but mating systems and group composition show considerable flexibility, in particular in wild callitrichids (Garber et al., 2016; Goldizen, 1988; Solomon and French, 1997; Sussman and Garber, 1987). Reproductive success depends on the availability of alloparental care, which increases infant growth and survival, especially in common marmosets (Koenig, 1995; Rothe et al., 1993) but also in other callitrichid species (Sussman and Garber, 1987). After the first post-partum days, during which mothers typically are the primary caretakers in common marmosets (Koenig and Rothe, 1991; Mills et al., 2004), help is provided by fathers and other group members, who are mostly, but not exclusively, the adult and sub-adult offspring of the breeding pair, and who delay dispersal and help rearing their siblings (Digby et al., 2007; Garber, 1997; Goldizen, 1987b; Yamamoto et al., 2014).

During early infancy, helping behavior mostly consists of carrying the offspring, which bears high energetic costs to carriers (Schradin and Anzenberger, 2001). Nevertheless, caretakers

also compete over access to infants (Mills et al., 2004; Yamamoto and Box, 1997; Zahed et al., 2010), and particularly female helpers are not always tolerated by other group members to handle and carry infants as much as they attempt to (Albuquerque, 1999; Price, 1991). Hence, individual infant-carrying contributions may not necessarily correspond to intrinsic motivational levels, especially if more caretakers than infants are available. During later infancy until juvenile age, carrying continually decreases and is complemented by food provisioning to immatures. In contrast to infant-carrying, food provisioning can always be performed ad libitum and is usually not constrained by other group members. During peak provisioning periods, adults share up to 63 % of provided food items with immatures, and 40 % of these food transfers occur proactively (Martins et al., in preparation), i.e. are initiated by the adult who offers the food to the immature (Brown et al., 2004). Non-reproductive helpers show particularly high levels of proactive food sharing (48 %) during that time. Alloparents thus seem to have high intrinsic care-taking motivation, and, in fact, helping in subordinates is not enforced by breeders through coercion or punishment (Snowdon and Cronin, 2007).

In marmoset mothers, labor and lactation as well as maternal infant-care after birth are accompanied by a number of hormonal changes: Towards labor, estradiol and progesterone levels decrease drastically (Chambers and Hearn, 1979) and are linked to post-partum sexual cycling independently of lactation (Kholkute, 1984), whereas prolactin levels increase and remain elevated during lactation (McNeilly et al., 1981). Reproduction-related OT patterns in callitrichid monkeys may be comparable to those of other primates, where plasma OT is elevated during late pregnancy and parturition (Hirst and Thorburn, 1996; Novy and Haluska, 1994), and during lactation in rhesus monkeys (*Macaca mulatto*) (Amico et al., 1990) but not in Cynomolgus monkeys (*Macaca fascicularis*) (Morris et al., 1980).

The hormones mentioned above are also involved in maternal care-taking behaviors and motivation: Sex steroids positively affect maternal responsiveness during late pregnancy in marmosets and tamarins (Pryce et al., 1993). Pre-partum estrogen levels are also positively linked to subsequent maternal care-taking behavior in tamarins (Pryce et al., 1988), macaques (Bardi et al., 2003), and humans (Fleming et al., 1987); see also Maestripieri (2001a), Maestripieri (2001b), and Saltzman and Maestripieri (2011), but conflicting results were described for common marmosets (Pryce et al., 1995), black-tufted marmosets (Fite and French, 2000), gorillas (Bahr et al., 2001), and baboons (Bardi et al., 2004); see also Maestripieri (2001a)

and Saltzman and Maestripieri (2011). Primate maternal behavior can also be influenced by stress-related hormones and neuropeptides (Saltzman and Maestripieri, 2011), whereas there is no indication for a positive link of prolactin and maternal care based on the limited available evidence in marmosets (Saltzman and Abbott, 2005). OT seems to be fundamentally involved in motivational priming during mother-infant bonding in mammals (Carter, 1998; Maestripieri, 2001b) and it is positively involved in maternal behavior in rats (Fahrbach et al., 1984; Pedersen et al., 1994) and sheep (Kendrick et al., 1987), but such effects have not been studied in primates yet.

The neuroendocrine hypothesis suggests that hormonal priming may generally play a vital role in the mediation of infant-care motivation, which may provide an important complement to parenting experience, thus being particularly valuable for inexperienced mothers but also alloparental caretakers (Pryce, 1993). However, evidence for such effects in primates is still very limited and partly contradictory. Positive evidence related to non-maternal care exists for example for tamarin fathers, who show changes of testosterone, estradiol, and glucocorticoid levels in the pre-partum period as well as during infant-care, possibly preparing males for the impending birth and parenting role (Ziegler and Snowdon, 2000; Ziegler et al., 2004; Ziegler et al., 1996). Prolactin is also positively linked to infant-care in marmoset fathers and helpers (Dixson and George, 1982; Mota et al., 2006; Mota and Sousa, 2000; Roberts et al., 2001; Schradin et al., 2003), but these studies suggest that prolactin increases in response to infant-contact and -carrying rather than promoting such behaviors based on motivation-stimulating effects. Accordingly, experienced marmoset fathers could express normal paternal care even if prolactin was suppressed (Almond et al., 2006). In contrast, OT has been shown to stimulate alloparental infant-care motivation in different mammal species: In rodents, peripheral OT administration facilitated alloparental pup-retrieval, -licking, and -grooming in females (Bales et al., 2007), and OT-antagonist inhibited such behaviors in males (Bales et al., 2004). Peripheral OT administration also enhanced guarding, feeding, and association with pups in meerkats (Madden and Clutton-Brock, 2011), and intracerebroventricular OT administration facilitated paternal food sharing in marmosets (Saito and Nakamura, 2011a). However, it remains to be established whether OT is also positively linked to alloparental behavior and motivation in non-reproductive primate helpers, and whether this link is reflected in endogenous OT responses, since the existing evidence mainly focusses on exogenous OT effects.

The aim of this study was to assess the role of OT in care-taking behavior in family groups of cooperatively breeding marmosets, with particular focus on the relationship between OT and care motivation in non-mothers. We longitudinally followed five family groups of common marmosets over a total of eight reproductive cycles. During each reproductive cycle, we collected baseline OT levels from morning void urine and data on care-taking behaviors (infant-carrying, -licking, -grooming, and proactive food sharing) and affiliative behaviors between adult group members (grooming and huddling), over a total period of 12 weeks (starting one week before birth).

First, we investigated whether urinary OT levels increased immediately after infant-birth in mothers and other adult caretakers, which would be consistent with the neuroendocrine priming hypothesis (Pryce, 1993). Based on OT functions in mammalian birth (Kendrick, 2000; Landgraf et al., 1983; Nissen et al., 1995) and lactation (Uvnäs-Moberg et al., 2001), we expected OT levels of breeding females to be elevated after birth and during lactation until infant-weaning. Higher OT levels in response to the presence of new-born offspring were also expected in marmoset fathers, based on findings of positive peripheral OT responses in human parents (Feldman et al., 2011; Gordon et al., 2010a; Nissen et al., 1995). Since non-reproductive helpers in marmosets also show high levels of alloparental care (Digby et al., 2007; Goldizen, 1987b), we predicted a positive OT response also in helper individuals of both sexes.

Second we analyzed to what extent urinary OT patterns reflect care-taking behaviors, while taking affiliation with other adults, infant age, and care-taking experience into account. We also compared the effects in early and late infancy, because frequencies and importance of the different infant-directed behaviors change over time. The facilitating effects of exogenous OT on paternal food transfer in marmosets (Saito and Nakamura, 2011a) and alloparental behaviors in other mammals (Bales et al., 2007; Madden and Clutton-Brock, 2011) suggest that OT may be positively associated with intrinsic care-taking motivation. We therefor expected urinary OT levels to be positively linked in particular to those care-taking behaviors that can be freely expressed by all individuals motivated to do so. During early infancy, this arguably mainly includes infant-licking and -grooming, since the immobile infants cannot be carried simultaneously by all motivated caretakers, but infants can be licked and groomed also on the backs of other caretakers. Furthermore, compared to licking and grooming, carrying is a more passive behavior once the infant sits on the carrier and may thus be less related to OT. During

late infancy, carrying and licking decrease continuously and food sharing becomes more important. In particular proactive food sharing (Brown et al., 2004), which is initiated by the food possessor rather than a begging immature, was expected to be positively linked to OT during this period because it is dependent on intrinsic proactive motivation (Jaeggi and Gurven, 2013) and can be performed ad libitum by all motivated caretakers.

4.3. Methods

4.3.1. Study animals

We studied five marmoset family groups (26 individuals) over a total of eight reproductive cycles. Two groups (ten individuals) were sampled repeatedly over different reproductive cycles during this study. Reproductive cycle order, group identity, size, and composition, as well as individual identity, sex, status (breeder or helper), age, and care-taking experience (number of raised offspring for breeders and the number of raised siblings for helpers) are listed in supplementary table S 4.3. Juvenile group members from previous reproductive cycles, who were younger than 10 months and did not yet participate in alloparenting of new born offspring, were not part of this study and are not listed in table S 4.3. One sub-adult individual (Nikita) was actively participating in alloparenting in reproductive cycle 8 and was hence included in the analysis with the other (adult) caretakers. All groups were housed in standardized enclosures (depending on group size, one or multiple basic cage units; each measuring 2.4 m height x 1.5 m depth x 0.8 m width). All enclosures were connected to spacious outdoor areas and equipped with a sleeping box, a water dispenser, several wooden climbing structures, an infrared lamp and a mulch floor. The animals were housed under natural light with additional artificial light on a 12 h/12 h light–dark cycle and UV light (300W). Their diet consisted of a vitamin and calcium-enriched porridge in the morning, fresh fruits and vegetables over midday, as well as gum and mealworms in the afternoon, and water was available ad libitum. A special cage unit that was only accessible in the morning during urine collection (Anzenberger and Gossweiler, 1993) was attached to each home cage. On urine sampling days, mealworms were fed in the urine cages in the morning instead of afternoon.

4.3.2. Urine sampling and OT detection

Baseline OT levels were detected from individual morning urine samples that were collected during each reproductive cycle. For each adult group member, urine was collected two times per week over a period of six to 12 consecutive weeks, starting one week before birth. The sampling was restricted to morning-void urine, in order to measure hormonal baseline values and to minimize confounding effects of circadian rhythms. Urine was collected non-invasively either in a urine cage or with a plastic cup in the home cage, as described elsewhere (Finkenwirth et al., 2015). Urine samples were labelled right after collection and stored immediately at -20°C in 1 ml portions until analysis.

OT was measured in the endocrinology laboratory of the department of Primatology at the Max Planck Institute of Evolutionary Anthropology, Leipzig, Germany, using commercial OT assay kits (Assay Designs, Cat no. ADI-900-153A-0001). The procedure was developed and validated by Seltzer and Ziegler (2007) and Snowdon et al. (2010), and slightly adapted for our purpose, as previously described in Finkenwirth et al. (2015). A detailed protocol is provided in the supplementary material. Because a new antibody component was developed by Enzo Assay Designs and provided with the OT assay kit during our study, OT measurements of reproductive cycle 1-3 and 4-8 were based on different OT assays kits with slightly different binding capacities (assay A and B). OT concentrations measured with assay B were approximately two times higher than with assay A. We therefore measured 33 samples with both kits, and found OT concentrations to be highly correlated between the two assays (Pearson correlation: $N = 33$, $r = 0.82$, $p < 0.001$), and quality criteria of both assays were very similar. Mean intra-assay coefficients of variation for high (250 pg/ml) and low (50 pg/ml) OT standards were 9.59 % and 13.76 % for assay A, and 6.51 % and 14.36 % for assay B, respectively. Mean inter-assay variation coefficients of variation for high and low OT standards were 12.48 % and 19.26 % for assay A, and 8.23 % and 13.56 % for assay B, respectively. Prior to statistical analysis, all OT concentrations were corrected for creatinine levels to control for variable urine concentration and ln-transformed to reach normal distribution. In order to analyze OT levels across all reproductive cycles despite the assay-dependent variation in OT measurements, ln-transformed OT concentrations were also z-standardized within each assay (Z ln pg OT/mg Crt). Information on original OT measurements (pg/mg Crt) is provided in supplementary table S 4.3 in form of individual mean ± SD OT levels.

4.3.3. Behavioral data collection

Along each reproductive cycle, we collected data on care-taking behaviors, adult-affiliation, and proactive food sharing rates. A detailed sampling protocol of behavioral and hormonal data along the eight reproductive cycles is provided in supplementary table S 4.4. Care-taking behaviors included infant-carrying, which was recorded daily (between 8 am and 5 pm) in hourly group scans during 100 days after birth, and infant-licking and -grooming, which was recorded two to three times per week as all occurrences in continuous group observations of one hour (data available for birth 4-8). Adult-directed affiliative behaviors included grooming (picking the fur or skin of a partner with hands or mouth) and huddling (resting in direct body contact), which was recorded as all occurrences along with the infant-directed behavior during the continuous group observations. Observation sessions were equally distributed between morning and afternoon (9–12 am or 1–5 pm). For analysis, adult-grooming and -huddling were combined into one variable (data available for all groups). All observed behaviors and carrying scans were corrected for observation time or the number of scans, respectively, and carrying is expressed as percentage of the total number of scans (100*scans carried/total scans). Finally, all affiliation variables (infant-licking and -grooming and adult-affiliation) were ln-transformed in order to reach normal distributions prior to statistical analysis.

Proactive food sharing was characterized by i) the donor keeping the food in the mouth or hand while emitting food calls and waiting for a recipient and ii) by the absence of begging from recipients (Brown et al., 2004). Proactive food sharing was assessed experimentally two to three times per week (between 9–12 am or 1–5 pm) for each adult caretaker in a group. To do so, a specific donor received three to five preferred food items (small crickets) one after another, and we recorded the frequencies and characteristics of sharing (direction, vocalizations, begging intensity, pro- and reactivity, see also (Martins et al., in preparation). After receiving the food item, donors usually first moved into distance of the group and then either started to eat the food themselves or to initiate proactive food sharing with food calls. If donors were harassed by potential recipients prior to sharing or if they shared food only after begging by recipients, we recorded this behavior as resisted or reactive sharing, which was not included in the present analysis. To avoid saturation of infants and keep their interest in food items high, we tested only up to three adult caretakers per group and day. Proactive food sharing rates were expressed as

percentage of the total number of food items received (100 * N food items shared proactively/N food items received).

4.3.4. Statistics

In order to investigate the relationship between urinary OT levels and infant birth, care-taking behaviors, adult-affiliation, and infant age, we performed several linear mixed-effect models with restricted maximum likelihood estimation (R version 3.1.3, lme package). All models included the random factors of individual nested in family group, and reproductive cycle nested in family group, to control for the repeated occurrence of the same individuals across different reproductive cycles (relevant for individuals in the groups 'Nina' and 'Lancia', see supplementary table S 4.3).

First, we tested whether OT increased after infant-birth (model 1), by comparing data from the late pre-partum period (one week before birth) with the early post-partum period (weeks zero and one). Sampling period (pre- and post-birth), status (breeder and helper), and sex (female and male) were included as fixed factors, and the model was based on individual mean values from all 26 individuals of the eight reproductive cycles (N=70 samples, missing values from week -1 of two groups).

Second, we investigated longitudinal changes in urinary OT levels and care-taking behaviors (infant-carrying, -licking, -grooming, and proactive food sharing) and the link between both over 11 weeks after birth. We first compared overall changes in care-taking behaviors between early (week 0-5) and late infancy (week 6-11) based on individual mean values for each time block. To do so, we performed four linear mixed models including infant-carrying (model 2), -licking (model 3), -grooming (model 4), or proactive food sharing (model 5) as dependent variable, sex, status, and infant age as fixed factors (supplementary tables S 4.5). Infant age was a block variable with two levels (block 1 = week 0-5, block 2 = week 6-11 post-partum). For infant-carrying, these changes were also analyzed separately for status-sex groups, using paired samples t-test and Cohen's d for effect size estimation. This was not possible for infant-licking and -grooming due to limited sample size.

Third, we tested the link between weekly mean OT values, care-taking behaviors (infant-carrying, -licking, -grooming, and proactive food sharing), and adult-affiliation, based on the data from reproductive cycles 4-8 (N=236 samples from 22 individuals; see supplementary table

S 4.4). To do so, we first performed a full model (model 6) including all behavioral variables, status, sex, infant age, and individual care-taking experience as fixed factors (supplementary table S 4.5). Care-taking experience was the number of raised offspring for breeders and the number of raised siblings for helpers. We also included the interaction between status and sex, since effects in female breeders, male breeders, female helpers, and male helpers may differ. Second, in order to evaluate the changing impact of behavioral variables on OT during infant development, we performed separate analyses for early (model 7) and late infancy (model 8). We tested different models that included all factors of the full model, as well as biologically meaningful interactions. The best-fitting model was selected based on the Akaike information criterion (AIC) estimation. In all models, approximate normality and homogeneity of residuals was assessed by visual inspection of residuals plotted against fitted values and a qq-plot. All model assumptions were met.

4.4. Results

4.4.1. Comparing pre- and post-birth OT levels

In breeders as well as helpers, urinary OT levels increased within the first days after the birth of new infants (figure 4.1). This increase was highly significant ($t=4.98$, $p < 0.0001$, model 1, table 4.1). The model also showed strong effects of status and sex as well as an interaction of status*sex, as the highest OT levels were present in breeder females (figure 4.1).

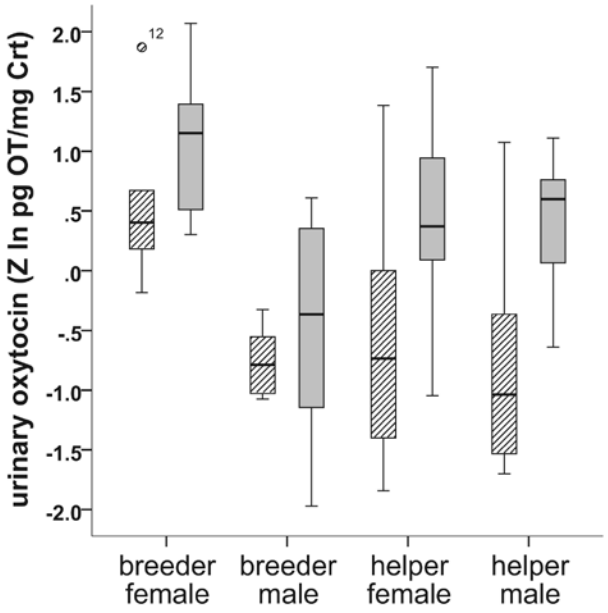

Figure 4.1: Mean urinary oxytocin levels in the pre- and post-partum period. Oxytocin (Z ln pg OT/mg Crt) levels in breeder females are significantly higher than in all other status-sex classes, and post-partum (filled bars) oxytocin increased significantly compared to pre-partum (dashed bars) oxytocin in breeder females, breeder males, helper females, and helper males (see model 1, table 4.1).

Table 4.1. Linear mixed-effects model fit by REML. Analysis of urinary oxytocin in the late pre-partum and early post-partum periods (model 1). Parameter estimates: factor levels with bars are compared to the remaining factor levels. Bold: $p < 0.05$. Late pre-partum period: week -1; early post-partum period: week 0-1 (N=70 samples from 26 individuals in 8 reproductive cycles).

fixed factor	F	df	p-value	factor level	estimate	s.e.	t	P
intercept	0.04	1	0.842		-0.75	0.39	-1.92	0.062
sampling period	**26.06**	**1**	**<0.0001**	**post-partum**	**0.96**	**0.19**	**4.98**	**<0.0001**
				pre-partum	-	-	-	-
status	**0.15**	**1**	**0.707**	**helper**	**-0.79**	**0.27**	**-2.93**	**0.009**
				breeder	-	-	-	-
sex	**6.32**	**1**	**0.022**	**male**	**-1.32**	**0.30**	**-4.41**	**<0.001**
				female	-	-	-	-
status*sex	**13.20**	**1**	**0.002**		**1.40**	**0.38**	**3.63**	**0.002**

4.4.2. OT and care-taking behaviors

Over the total study period of 12 weeks, starting one week prior to birth, mean urinary OT levels in breeder females, breeder males, helper females, and helper males underwent substantial longitudinal changes (figure 4.2, data from all 8 reproductive cycles). In all classes of animals, a significant OT peak occurred in the early post-partum period (see also table 4.1, model 1). Breeder females generally showed the highest OT levels (tables 4.1 & 4.2, models 1 & 7) and their post-partum OT remained on a high plateau that only declined towards week five, when infants start to eat solid food regularly and lactation decreases (indicated by the arrow in figure 4.2).

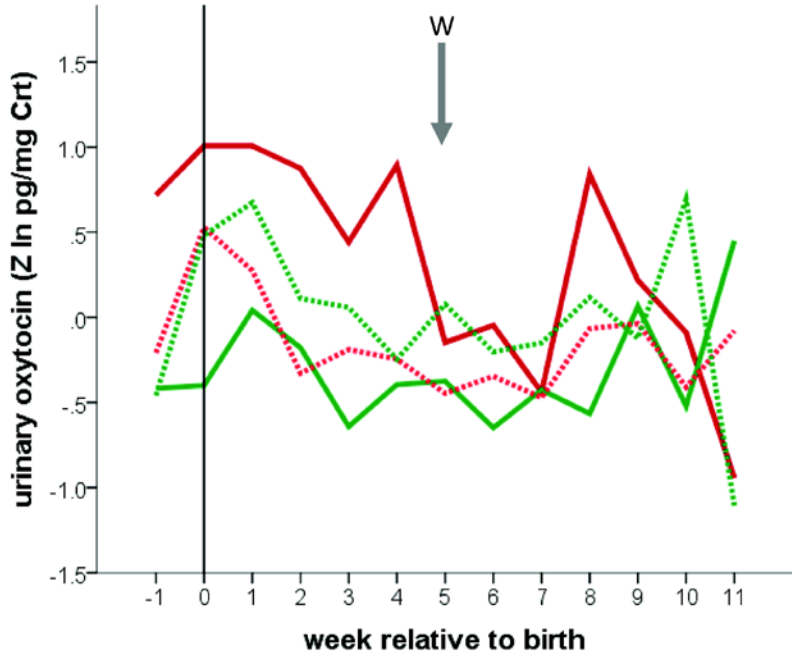

Figure 4.2: Longitudinal changes of urinary oxytocin levels over 12 weeks around birth (vertical line). A major increase of oxytocin (Z ln pg/mg Crt) occurs around infant-birth in female breeders (red solid line), male breeders (green solid line), female helpers (red dotted line), and male helpers (green dotted line). The arrow indicates the onset of infant-weaning and solid food ingestion, which coincides with the major drop in breeder female OT levels.

Longitudinal changes of care-taking behaviors including infant-carrying, -licking, -grooming, and proactive food sharing over 11 weeks after birth are shown in figure 4.3A-D. Mean rates of carrying, licking and grooming were highest during early infancy compared to late

infancy (carrying: $t = -5.29$, $p < 0.001$, model 2; licking: $t = -6.83$, $p < 0.001$, model 3; grooming: $t = -2.25$, $p = 0.030$, model 4; supplementary table S 4.5), following a decreasing trend. Infant-carrying rates of breeders and helpers showed compensating patterns over time: Whereas carrying decreased from early to late infancy in breeder females ($t(6) = 9.03$, $p < 0.001$, $d = 2.85$), breeder males ($t(7) = 5.73$, $p = 0.001$, $d = 2.15$), and helper males ($t(11) = 2.89$, $p = 0.015$, $d = 1.26$), it showed a strong increasing trend in female helpers, who only reached peak levels of carrying in week seven post-partum ($t(12) = -1.77$, $p = 0.10$, $d = -0.51$). Mean proactive food sharing increased significantly to peak levels after week five post-partum (during late infancy) in all individuals ($t = 9.52$, $p<0.0001$, model 5; supplementary table S 4.5), which was congruent with the transition of the infants' diet from milk to solid food and with increasing infant mobility. Particularly high levels of proactive food sharing were reached in female and male helpers as well as male breeders between week seven and nine, and this time was also characterized by a new increasing trend in urinary OT levels in breeders as well as helpers (figure 4.2).

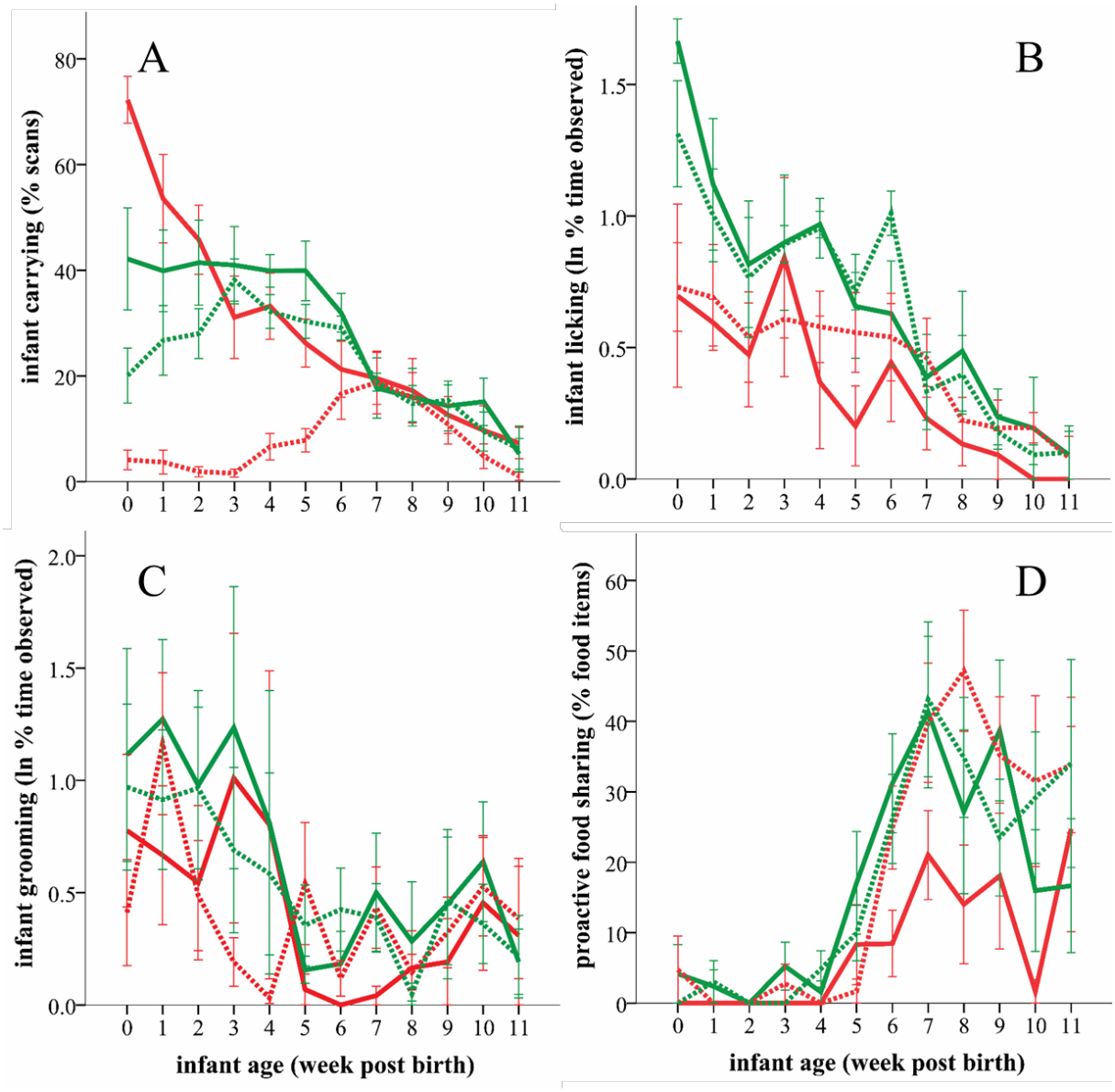

Figure 4.3: Longitudinal changes of infant-carrying (A), -licking (B), -grooming (C), and mean proactive food sharing (D), split by breeder females (red solid lines), breeder males (green solid lines), helper females (red dotted lines), and helper males (green dotted lines).

The relationship between individual urinary OT levels, care-taking behaviors, and adult-affiliation over the total study period of 11 weeks after birth was first assessed in a full linear mixed model (model 6, supplementary table S 4.5). OT was significantly higher in breeders than helpers and in females than males. The interaction effect status*sex reflects the higher OT levels in female breeders compared to other individuals (figures 4.1 and 4.2). OT decreased from early

towards late infancy, as indicated by the negative effect of infant age. Among the care-taking behaviors, proactive food sharing had a positive effect on OT, but no effect was found for infant-carrying, -licking, and -grooming. Negative effects emanated from adult-affiliation and individual parenting experience (number of raised offspring or siblings).

To evaluate the changing impact of care-taking behaviors and adult-affiliation on OT during infant development, we analyzed the data separately for early and late infancy. During early infancy, we found a strongly positive effect of infant-licking, and higher OT levels in females compared to males and in breeders compared to helpers (table 4.2, model 7). Affiliation with adults had a negative effect. During late infancy, breeders still had higher OT levels than helpers, but the effects of infant-licking, sex, and adult-affiliation effects vanished. Instead, proactive food sharing was positively linked to OT levels during this period (table 4.2, model 8).

Table 4.2: Linear mixed-effects model fits by REML. Factors influencing urinary oxytocin during early and late infancy. Parameter estimates: factor levels with bars are compared with remaining factor levels. Bold: $p < 0.05$. Early infancy: post-partum week 0-5 (model 7); late infancy: post-partum week 6-11 (model 8). (N=236 samples from 22 individuals in 5 reproductive cycles).

model	fixed factor	F	df	p-value	factor level	estimate	s.e.	t	P
model 7, early infancy	intercept	0.38	1	0.538		0.94	0.41	2.28	0.025
	status	0.45	1	0.513	**helper**	**-0.85**	**0.34**	**-2.48**	**0.026**
					breeder	-	-	-	-
	sex	1.79	1	0.200	**male**	**-0.96**	**0.33**	**-2.93**	**0.010**
					female	-	-	-	-
	status*sex	4.21	1	0.058		0.91	0.45	2.05	0.058
	adult-affiliation	**18.18**	**1**	**<0.0001**		**-0.28**	**0.07**	**-4.10**	**0.0001**
	proactive food sharing	2.17	1	0.144		1.65	1.04	1.59	0.115
	infant-licking	**7.31**	**1**	**0.008**		**0.22**	**0.08**	**2.89**	**0.005**
	infant-grooming	0.13	1	0.720		-0.10	0.13	-0.73	0.469
	infant-carrying	0.14	1	0.708		-0.07	0.08	-0.80	0.424
model 8, late infancy	**intercept**	0.00	1	0.944		1.07	0.69	1.55	0.126
	status	0.13	1	0.722	**helper**	**-1.18**	**0.54**	**-2.17**	**0.048**
					breeder	-	-	-	-

sex	0.09	1	0.771	male	-0.58	0.50	-1.15	0.272
				female	-	-	-	-
status*sex	4.62	1	0.050		1.09	0.63	1.74	0.103
care-taking experience	**5.30**	**1**	**0.024**		-0.08	0.08	-0.99	0.328
adult-affiliation	1.31	1	0.256		-0.090	0.12	-0.76	0.452
proactive food sharing	0.96	1	0.330		**1.82**	**0.81**	**2.24**	**0.028**
infant-licking	0.13	1	0.719		-0.08	0.16	0.51	0.615
infant-grooming	0.16	1	0.690		-0.15	0.21	-0.70	0.484
infant-carrying	1.40	1	0.240		-0.16	0.11	-1.43	0.156
proactive food sharing*care-taking experience	2.84	1	0.096		-0.31	0.19	-1.68	0.096

4.5. Discussion

This study systematically investigated longitudinal changes of urinary OT related to care-taking behaviors over three months after birth in group-living marmoset breeders and alloparental helpers. Specifically, we tested whether OT increased in breeders and helpers directly after infant birth, and to what extent changes in OT reflected the changing needs during infant development and care-taking motivation.

First, we found that in all marmoset caretakers, OT levels increased immediately after the birth of new offspring. OT levels in the pre-partum week and early post-partum period were highest in female breeders, consistent with the general role of OT in parturition (Blanks and Thornton, 2003) and lactation (Uvnäs-Moberg et al., 2001). However, the post-partum OT increase in fathers and non-reproductive helpers suggests that the role of OT extends beyond maternal reproduction and is also linked to infant-care, in both parents and alloparents. This is consistent with the neuroendocrine hypothesis that emphasizes the relevance of hormonal priming mechanisms underlying infant-care motivation (Pryce, 1993).

Second, we found that during early infancy, longitudinal changes of post-partum OT levels were positively linked to infant-licking, and during late infancy, to proactive food sharing, in both breeders and helpers. Furthermore, during early infancy - the most intense time of infant-care - adult-affiliation was negatively correlated with urinary OT levels, arguably reflecting time-budget trade-offs between infant-care and affiliation with other adults.

The diverging patterns of OT effects in early and late infancy correspond to the changing developmental needs of the infants: licking occurs mainly with young infants and food sharing with older infants. In early infancy, infant-carrying and -grooming are frequent too, but they are not related to OT. Infant-licking, more than -grooming or -carrying, arguably involves highly intense chemical stimulation, which might be responsible for its strong link with OT. Physical contact and effort during infant-grooming or -carrying, however, did not exert any effect on OT. Together with the strong effect of proactive food sharing on OT, this indicates that OT levels during periods of intense infant-care do not simply result from physical contact, as suggested for prolactin (Mota et al., 2006). Rather, OT may be involved in the motivational regulation of infant-care, which is also consistent with stimulating effects of exogenous OT-administration on maternal (Kendrick et al., 1987; Pedersen et al., 1994) and non-maternal (Bales et al., 2007; Madden and Clutton-Brock, 2011; Saito and Nakamura, 2011a) care-taking in mammals. Nonetheless, the causal interpretation of effect directions in our findings is limited due to the non-invasive study design. Finally, potential motivation stimulating OT effects and OT responses to chemical or physical stimuli may also be intertwined bi-directionally, especially if interactions with other hormones are involved.

The hypothesis that OT may be positively associated with care-taking motivation is particularly supported by the positive link of OT and proactive food sharing during late infancy. Proactive food sharing, the only correlate of OT in late infancy, is a care-taking behavior that can be performed almost without constraint, and is thus thought to be a direct indicator of an intrinsic motivation to care (note that food sharing was assessed experimentally, which also controlled for the possibility of infant-satiation). However, infant-licking during early infancy may also be a good proxy for care-motivation - more so than carrying or grooming. Carrying was not possible for all motivated caretakers at the same time, because a maximum of two infants per group were available. Furthermore, infant-carrying rates may also be influenced and biased by other social constraints, e.g. female breeders could be protective and restrict the access to infants (mostly towards female helpers), arguably to minimize the risk of infanticide (Albuquerque, 1999; Digby, 1995a; Yamamoto et al., 2010; Yamamoto et al., 2009). Finally, older and more mobile infants play an increasingly active role in choosing their carriers. Grooming levels may be a weak proxy for care motivation because they may not exclusively represent infant-directed

grooming, since infants were often groomed on the back of other adult carriers, and adult-directed grooming could not always be clearly excluded in the observation.

During the first post-partum weeks, affiliation among adults was negatively associated with urinary OT levels in all individuals. This result is surprising given that OT typically shows a positive rather than negative association with affiliative behaviors (Crockford et al., 2013, Insel, 2010, Snowdon et al., 2010; but see Bartz et al., 2011, De Dreu, 2012, Mustoe et al., 2015). However, this effect may reflect a simple time-budget trade-off and altered social dynamics in groups with new dependent offspring. During early infancy, social interactions are mainly determined by the intense care for infants, leaving less time to engage in affiliation with other group members in general. It may be particularly difficult to engage in affiliation with a specific partner since the probability is even smaller that both partners of a specific dyad are available. This is relevant in the face of recent findings that in chimpanzees (Crockford et al., 2013) and marmosets (Finkenwirth et al., 2015) urinary OT responses to adult-adult affiliation are dyad-specific and predominantly occur in strong bond dyads. Furthermore, individuals with high levels of adult-adult affiliation are more likely to engage in infant-care (chapter 5, Finkenwirth and Burkart, in preparation-a). Together, this thus suggests that the negative effect in our data reflects a lack of affiliative interactions with stronger bonded or preferred group members.

Finally, in the full model, we also found a negative effect of care-taking experience on OT. This effect could tentatively be interpreted as a customization to infant cues, leading to decreasing OT responses in more experienced caretakers. Experience might potentially also complement motivation-stimulating OT effects, in that motivation-stimulation is rather important for less experienced individuals, such as alloparental helpers. However, especially in primiparous mothers, care-motivation should be facilitated and maintained independently of previous alloparenting experience (e.g. via hormonal stimulation), since maternal care is most important during the early post-partum period (Koenig and Rothe, 1991; Mills et al., 2004). This is also evident from experience-independent maternal performance in marmosets (Tardif et al., 1984). It is important to note, however, that we used a combined measure of experience for helpers and breeders, and we cannot exclude the possibility that parenting experience of breeders is qualitatively different from alloparenting experience of non-reproductive helpers. Furthermore, helpers had significantly less experience than breeders (median experience in breeders and helpers was 4 and 1.5 raised infants, respectively; Mann-Whitney $U = 23$, $N_{breeders} = 16$, $N_{helpers} =$

26, $P < 0.001$, $Z = -4.88$, $r = 0.75$), and we had no inexperienced breeders in the sample. Hence, the experience effects reported here should be evaluated with caution, and a potential interaction between motivational and experience-related compensating OT effects requires further investigation.

In this study we chose a non-invasive method of OT sampling. Crockford et al. (2014) review and discuss the relevance of peripheral OT measures for studying the dynamics of social interactions and relationships with particular emphasis on urinary OT. Besides its effects in social bonding and affiliation in mammals (Lim and Young, 2006), peripheral OT is involved in female reproduction (labor and milk letdown) (Blanks and Thornton, 2003; Uvnäs-Moberg et al., 2001) and anxiety reduction (Olff et al., 2013). A broadening body of evidence indicates that these central and peripheral OT pathways can be coordinated (Carson et al., 2014; Carter et al., 2007; O'Byrne et al., 1990; Ross and Young, 2009; Wotjak et al., 1998) and may exert cross-linked effects (Ayers et al., 2011; Madden and Clutton-Brock, 2011; Witt et al., 1990). Other studies indicate independent control mechanisms of central and peripheral OT secretion (Amico et al., 1990; Rosenblum et al., 2002; Seckl and Lightman, 1987). However, a coordination of central and peripheral OT effects may also be facilitated indirectly, e.g. via steroid hormones (Bos et al., 2012; McCarthy, 1995; Ochedalski et al., 2007) and bidirectional feedback mechanisms with peripheral organs and body states (Goodson and Thompson, 2010). Such a coordination may also be dependent on the involved stimulating brain regions (Martínez-Lorenzana et al., 2008). In primates, urinary OT levels have been found to be related to affiliative (Crockford et al., 2013; Finkenwirth et al., 2015; Wittig et al., 2014) and socio-sexual interactions (Moscovice and Ziegler, 2012; Snowdon et al., 2010) among group-living individuals. Accordingly, Crockford et al. (2014) suggested that peripheral OT measurements are indeed useful to capture central OT excretion or a coordinated release between central and peripheral effects in primates. However, experimental studies looking at exogenous OT effects on care-taking behaviors and motivation would be valuable to better understand the effects and potential causal mechanisms related to the findings of our study.

4.6. Conclusion

Our findings show that OT is positively associated with care-taking behaviors in group-living marmoset parents and alloparents. OT increased in all adult group members immediately

after the birth of infants. Consistent with the changing needs during infant development, OT was correlated with infant-licking during early infancy and with proactive food sharing especially during late infancy. OT did not simply reflect a physical response to care-taking effort, since there was no link to infant-carrying. Rather, OT may be positively associated with care-taking motivation, which is arguably best quantified by proactive food sharing. Importantly, these effects were not only present in breeders but also in alloparental helpers, which makes these findings valuable for a better understanding of the regulation of alloparental care in marmosets, and perhaps also of other cooperatively breeding species such as humans (Burkart and Finkenwirth, 2014). Future studies will have to integrate these findings with effects of other hormones, such as prolactin, that are also positively involved in the regulation of care-taking behavior and that might potentially interact with and compensate OT effects.

4.7. Acknowledgements

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4.8. Supplementary material

Table S 4.3: Individual information and sampling order. Reproductive cycle number (RC Nr), individual group membership, name, sex, status, age, care-taking experience (N raised infants), and mean oxytocin values of all 26 individuals that were part of this study.

RC Nr	group id	individual	sex	status	age	experience (N raised infants)	oxytocin measurement pg OT /ml Crt (mean ± SD)	assay
1	Lancia	Lancia	female	breeder	9.86	8	80.13 ± 41.66	A
	Lancia	Lexus	male	breeder	9.96	8	29.64 ± 12.43	
	Lancia	Lea	female	helper	4.89	2	42.02 ± 45.49	
	Lancia	Larissa	female	helper	4.22	0	21.45 ± 7.38	
	Lancia	Leon	male	helper	4.22	0	26.72 ± 9.84	
2	Mina	Mina	female	breeder	6.01	8	192.33 ± 191.02	
	Mina	John	male	breeder	5.34	7	19.36 ± 8.03	
	Mina	Mibba	female	helper	3.07	0	40.87 ± 58.33	
	Mina	Membo	male	helper	3.07	0	38.61 ± 31.73	
3	Nina	Nina	female	breeder	6.01	3	186.52 ± 229.32	
	Nina	Lex	male	breeder	6.01	3	76.44 ± 43.38	
	Nina	Nigg	male	helper	3.49	1	19.51 ± 8.45	
	Nina	Nari	male	helper	3.49	1	26.29 ± 17.40	
	Nina	Nala	female	helper	3.05	0	19.22 ± 5.54	
4	Nina	Nina	female	breeder	6.44	4	106.19 ± 71.67	
	Nina	Lex	male	breeder	6.44	4	76.44 ± 43.38	
	Nina	Nigg	male	helper	3.92	2	122.61 ± 166.81	
	Nina	Nari	male	helper	3.92	2	120.35 ± 40.40	
	Nina	Nala	female	helper	3.48	1	106.79 ± 45.95	
5	Lancia	Lancia	female	breeder	10.60	10	79.16 ± 38.86	B
	Lancia	Lexus	male	breeder	9.70	10	46.08 ± 36.13	
	Lancia	Lea	female	helper	5.62	4	76.27 ± 61.69	
	Lancia	Larissa	female	helper	4.96	2	130.69 ± 64.99	
	Lancia	Leon	male	helper	4.96	2	132.82 ± 90.84	
6	Kuta	Kuta	female	breeder	6.59	4	226.83 ± 80.38	
	Kuta	Jossua	male	breeder	6.56	4	295.46 ± 529.88	
	Kuta	Kos	male	helper	4.24	2	142.63 ± 100.74	
	Kuta	Kossa	female	helper	4.24	2	154.77 ± 107.84	
	Kuta	Kossua	female	helper	3.82	0	148.10 ± 105.37	
	Kuta	Kossu	male	helper	3.82	0	212.66 ± 127.37	
7	Jojoba	Jojoba	female	breeder	5.55	4	286.82 ± 308.59	
	Jojoba	Marvin	male	breeder	5.13	4	96.07 ± 61.01	
	Jojoba	Jet	male	helper	4.08	2	110.83 ± 133.10	
	Jojoba	Jupie	female	helper	3.67	0	131.83 ± 118.93	
	Jojoba	Jaja	female	helper	3.67	0	85.14 ± 72.99	
8	Nina	Nina	female	breeder	6.87	6	203.85 ± 13.67	
	Nina	Lex	male	breeder	6.87	6	121.11 ± 84.06	
	Nina	Nigg	male	helper	4.35	4	141.66 ± 121.09	
	Nina	Nari	male	helper	4.35	4	96.93 ± 47.57	
	Nina	Nala	female	helper	3.90	3	182.29 ± 95.71	
	Nina	Nikita	female	helper	0.85	0	57.85 ± 13.67	

Oxytocin ELISA protocol

Urine samples were run in duplicates at a volume of 200 µl. Prior to OT detection, samples were thawed, centrifuged, and extracted using solid phase extraction columns (Macherey-Nagel, 55–150 mm, WAT023501). Extraction columns were conditioned with 1 ml 100% methanol and 1 ml purified water. Samples were added (0.5 ml urine), washed with 1 ml 10% acetonitrile, 1% TFA (trifluoroacetic acid) in water, and eluted with 1 ml 80% acetonitrile in water. After the samples were dried, 300 µl 100% ethanol were added to the pellets, vortexted, and incubated for 30 minutes at room temperature. The ethanol was evaporated under a gentle stream of nitrogen and the samples were stored at -20°C until further use. To measure extracted samples on the ELISA plate, dried pellets were reconstituted in 250 µl assay buffer, centrifuged, and added to the microtiter plates according to the directions provided with the assay kit. The assay standard curve ranged from 7.5 to 1000 pg/ml and assay sensitivity was 7.5 pg/ml.

Table S 4.4: Data sampling protocol. Information on OT assay (OTA), birth number (BN), group, and sample size (number of individuals (NI)), as well as sampling protocols for urinary OT. For urine sampling, grey filling indicates sampled weeks.

OTA	BN	group	NI	Urine sampling (by week relative to birth)														
A				-3	-2	-1	0	1	2	3	4	5	6	7	8	9	10	11
	1	Lancia	5															
	2	Mina	4															
	3	Nina	5															
B	4	Nina	5															
	5	Lancia	5															
	6	Kuta	6															
	7	Jojoba	6															
	8	Nina	6															
Sum individuals			42	9	19	31	42	42	42	42	38	28	28	28	28	28	22	11

Tables S 4.5: Linear mixed effects model fits by REML. Parameter estimates: factor levels with bars are compared with remaining factor levels. Bold: $p < 0.05$. Early infancy: week 0-5, late infancy: week 6-11.

Model 2: Linear mixed effects model fit by REML on infant-carrying in early and late infancy. (N=81 samples from 26 individuals in 8 reproductive cycles).

fixed factor	F	df	p-value	factor level	estimate	s.e.	t	P
intercept	111.40	1	<0.0001		35.80	3.92	9.11	0
sampling period	**28.93**	**1**	**<0.0001**	**post-partum**	**-15.12**	**2.85**	**-5.29**	**0**
				pre-partum	-	-	-	-
status	**18.63**	**1**	**0.0004**	**helper**	**21.80**	**4.46**	**-4.88**	**0.0001**
				breeder	-	-	-	-
sex	**9.28**	**1**	**0.007**	male	-1.23	4.46	-0.24	0.806
				female	-	-	-	-
status*sex	**7.42**	**1**	**0.014**		**17.22**	**6.32**	**2.72**	**0.014**

Model 3: Linear mixed effects model fit by REML on infant-licking in early and late infancy. (N=55 samples from 22 individuals in 5 reproductive cycles).

fixed factor	F	df	p-value	factor level	estimate	s.e.	t	P
intercept	49.92	1	<0.0001		0.59	0.12	4.80	0.000
sampling period	**45.12**	**1**	**<0.0001**	**post-partum**	**-0.44**	**0.07**	**-6.83**	**0.000**
				pre-partum	-	-	-	-
status	0.62	**1**	0.444	helper	0.13	0.11	1.19	0.254
				breeder	-	-	-	-
sex	**13.11**	**1**	**0.003**	**male**	**0.33**	**0.13**	**2.60**	**0.020**
				female	-	-	-	-
status*sex	0.32	**1**	0.583		-0.09	0.16	-0.56	0.583

Model 4: Linear mixed effects model fit by REML on infant-grooming in early and late infancy. (N=67 samples from 26 individuals in 5 reproductive cycles).

fixed factor	F	df	p-value	factor level	estimate	s.e.	t	P
intercept	6.25	1	0.016		0.80	0.37	2.15	0.038
sampling period	**5.03**	**1**	**0.030**	**post-partum**	**-0.36**	**0.16**	**-2.25**	**0.030**
				pre-partum	-	-	-	-
status	0.02	1	0.892	helper	0.03	0.23	0.14	0.887
				breeder	-	-	-	-
sex	3.07	1	0.097	male	0.31	0.25	1.23	0.233
				female	-	-	-	-
status*sex	0.05	1	0.832		-0.07	0.32	-0.22	0.832

Model 5: Linear mixed effects model fit by REML on proactive food sharing in early and late infancy. (N=81 samples from 26 individuals in 8 reproductive cycles).

fixed factor	F	df	p-value	factor level	estimate	s.e.	t	P
intercept	72.64	1	<.0001		-5.16	4.05	-1.27	0.209
sampling period	**91.99**	**1**	**<.0001**	**post-partum**	**25.02**	**2.63**	**9.52**	**0.000**
				pre-partum	-	-	-	-
status	2.45	1	0.135	**helper**	**11.17**	**4.73**	**2.36**	**0.030**
				breeder	-	-	-	-
sex	0.55	1	0.468	male	9.62	5.28	1.82	0.085
				female	-	-	-	-
status*sex	3.01	1	0.099		-11.66	6.72	-1.73	0.100

Model 6: Linear mixed effects model fit by REML on urinary oxytocin over 11 weeks after birth. (N=236 samples from 22 individuals in 5 family groups).

fixed factor	F	df	p-value	factor level	estimate	s.e.	t	P
intercept	0.21	1	0.650		1.61	0.41	3.92	0.000
status	0.15	1	0.702	**helper**	**-1.30**	**0.31**	**-4.14**	**0.001**

				breeder	-	-	-	-
sex	2.04	1	0.173	**male**	**-0.87**	**0.26**	**-3.35**	**0.004**
				female	-	-	-	-
status*sex	**11.88**	**1**	**0.004**		**1.16**	**0.34**	**3.45**	**0.004**
infant age	0.67	1	0.414	**week 6-11**	**-0.37**	**0.16**	**-2.32**	**0.021**
				week 0-5	-	-	-	-
infant care experience	2.94	1	0.088		**-0.11**	**0.05**	**-2.30**	**0.022**
adult affiliation	**13.77**	**1**	**0.000**		**-0.20**	**0.06**	**-3.25**	**0.001**
proactive food sharing	2.81	1	0.095		**1.02**	**0.43**	**2.39**	**0.018**
infant carrying	0.25	1	0.621		-0.11	0.06	-1.86	0.065
infant grooming	0.65	1	0.423		-0.11	0.12	-0.92	0.357
infant licking	1.62	1	0.205		0.11	0.07	1.56	0.120

5. Consequences of relationship quality on infant-care behavior in group-living marmosets

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5.1. Abstract

Common marmoset monkeys engage in long-lasting monogamous bonds and raise their infants cooperatively, with the help of subordinate non-reproductive helpers. Even though helping can ultimately be understood to a large extent in terms of inclusive fitness benefits, considerable inter-individual variation in infant-care exists. The aim of this paper was to evaluate whether and how dyadic relationships and specific affiliative interactions with other group members affect individual cooperativeness in care-giving. In particular, we investigated whether allogrooming is used as a tool to serve individual strategies among marmoset group members, e.g. as payment for helping (from mothers to fathers, or from parents to helpers) or as payment for access to infants (from helpers to parents). Alternatively, relationship quality itself may determine individual cooperativeness, such that in more strongly bonded breeding pairs, both parents may engage more in care-giving, or that helpers with better social relationships to their parents help more. To test the pay-for-help, the pay-for-infant-access, and the relationship quality hypothesis, we followed five marmoset family groups over a total of eight reproductive cycles. We quantified affiliative behaviors (huddling and grooming), infant-carrying, and food sharing over six to 12 weeks, starting one week prior to birth. We found no evidence consistent with the idea that parents would pay helpers for helping, because pre-birth grooming from parents was not associated with more care-taking in helpers, and also no evidence for paying for infant-access, because pre-birth grooming from helpers to parents was not associated with increased access to infants. Dyadic relationships quality (indicated by dyadic mutual affiliation prior to infant-birth), however, had strong positive effects on infant-carrying and food sharing

both in breeders in breeder dyads, and in male helpers in breeder-helper dyads. These results suggest that grooming and affiliation are not used as a strategic tools in the context of infant-care. Rather, mutual relationship quality plays an important role and increases individual cooperativeness in group-living marmosets.

5.2. Introduction

Common marmosets live in small family groups that consist of a dominant breeding pair and non-reproductive helpers, who all together participate in the upbringing of dependent offspring (Goldizen, 1987b; Goldizen, 2003). The allomaternal care provided by fathers and helpers can ultimately be understood in terms of direct and inclusive fitness benefits (Emlen, 1995; Emlen et al., 1991; Huck et al., 2004). Nevertheless, considerable individual variation in infant-care exists (Burkart, 2015; Finkenwirth et al., 2016). An intriguing possibility is that individual variation in infant-care is linked to relationship quality, or to specific affiliative interactions that are used strategically to affect others' contribution to care-giving.

Good functional relationships between breeders, which are usually described as socially monogamous (Díaz-Muñoz and Bales, 2016), are ubiquitous in marmosets, where both mothers and fathers are directly involved in infant-care (Saito, 2015; Saito and Nakamura, 2011b). However, differentiated and stable relationships also occur in dyads other than the breeding pair, i.e. in breeder-helper dyads and in helper-helper dyads, and the relationship structure in marmoset families remains stable for at least six months (chapter 3, Finkenwirth and Burkart, in preparation-b; Finkenwirth et al., 2015). There is increasing evidence that in many primate species, good social relationships often involve cooperative interactions and are functionally adaptive (Seyfarth and Cheney, 2012; Silk, 2007a; Silk et al., 2009 & 2010), but so far, this question has not been addressed explicitly in marmosets monkeys, neither for breeding pairs nor for other dyads. We hypothesize that one potential function of good relationships in marmoset family groups may be that it increases individual cooperativeness.

A key element of the formation and maintenance of social relationships in primates are repeated affiliative interactions, especially allogrooming (Dunbar, 1991; Goosen, 1987). Dyadic affiliative interactions and grooming are meaningful estimators of the quality and value of relationships (Silk et al., 2006), as evident in many primates (Castles et al., 1996; Cooper et al., 2005; Fraser et al., 2008; Roubová et al., 2015), including marmosets, where strongly bonded

partners evidently groom each other more and show partner-specific oxytocin responses to affiliative interactions (Finkenwirth et al., 2015). On the other hand, grooming can also be used in a strategic way to enforce individual interests or as a market good in exchange for other commodities such as tolerance, coalitionary support, mating opportunities, and infant-access and -handling (Barrett and Henzi, 2001; Silk, 2005; Silk, 2007b). For instance, grooming can promote the formation of coalitions and agonistic support in males and females (Schino, 2007; Seyfarth, 1977), e.g. in chimpanzees (Nishida and Hosaka, 1996) and Japanese macaque (Ventura et al., 2006). Grooming can furthermore increase tolerance over food in tufted capuchin monkeys (Tiddi et al., 2011) and Japanese macaques (Ventura et al., 2006), reduce tension in long-tailed macaques (Schino et al., 1988), and can be used in conflict resolution (reviewed in Chadwick-Jones, 1998), e.g. in chimpanzees (Watts, 2006).

Hence, there are at least three alternatives for how affiliative interactions may be associated with contributions to infant-care, i.e. (i) the pay-for-help hypothesis, according to which grooming is used strategically by mothers and parents to pay other group members for helping, (ii) the pay-for-infant-access hypothesis, according to which grooming is used strategically by helpers to pay breeders for access to infants, or (iii) the relationship-quality hypothesis, according to which individuals with high quality relationships (characterized by high levels of mutual dyadic affiliation and grooming given to the partner) will contribute more to infant-care. These hypotheses lead to different sets of predictions regarding grooming patterns within families, and regarding the effect of grooming on participation in care taking, as summarized in table 5.1.

Table 5.1: Predictions of the three hypotheses with regard to expected affiliative interactions (received or directed grooming, and mutual dyadic relationship quality) on care-taking behavior in group-living marmosets.

Hypothesis		**Dyad type**	**Expected type of affiliative interaction**	**Expected effect on care-taking**	**When?**
Strategic effects	***Pay for help***	Breeder-Breeder	Directed grooming: females → males	**in males: positive correlation with grooming** *received from females*	Pre- and post-birth
		Breeder-Helper	Directed grooming: breeder → helper	**in helpers: positive correlation with grooming** *received from breeders*	Pre- and post-birth

	Pay for access to infants	Breeder-Helper	Strategic grooming: helper → breeder	**in helpers: positive correlation with grooming** *given to breeders* (only carrying)	Pre- and post-birth
Non-strategic effects	***Relationship quality***	Breeder-Breeder	Mutual dyadic affiliation:	**in both partners: positive correlation with** *mutual affiliation*	Pre-birth
			Directed grooming:	**in both partners: positive correlation with grooming** *given* to partner	Pre-birth
		Breeder-Helper	Mutual dyadic affiliation:	**in both partners: positive correlation** with *mutual affiliation*	Pre-birth
			Directed grooming:	**in both partners: positive correlation with grooming** *given* to partner	Pre-birth

First, directed grooming may be used to "pay" other group members for help during infant-care (pay-for-help hypothesis): In contrast to most other primates, grooming asymmetries in marmosets are typically shifted towards more grooming from dominant parents to subordinate helpers, which led to the hypothesis that mothers may groom fathers more and parents groom subordinate helpers more as incentive to stay and help rearing offspring (Lazaro-Perea et al., 2004; Löttker et al., 2007). This idea is supported by the finding that during pregnancy, wild tamarin mothers spent more time grooming male breeders and potential fathers compared to postpartum or non-reproductive periods, but note that mothers also received more grooming from fathers during this time (Löttker et al., 2007). Furthermore, Ginther and Snowdon (2009) found increased grooming levels from expectant tamarin mothers to adult sons, who had been most engaged in care-taking in the previous litter. Overall, this evidence is consistent with the idea that breeder females may actively strengthen the bonds with their mates, especially prior to birth, e.g. to keep breeder males attracted and committed to help. Lazaro-Perea et al. (2004) investigated grooming from mothers to daughters as reward for asymmetric services in wild groups of common marmosets. They found group-size dependent grooming of mothers to daughters, but no relation between participation in territorial defense and grooming received by daughters. Crucially, it has never been directly investigated whether directed grooming is indeed linked to subsequent helping in callitrichids. To evaluate the pay-for-help hypothesis, we will therefore test the predictions that more grooming (before and after birth of dependent offspring) is directed from mothers to fathers, and from parents to helpers than vice versa, and that received

grooming from mothers and fathers is positively linked to care-taking behavior in fathers and helpers, respectively.

Second, subordinates may use grooming to buy access to infants (and maybe tolerance during care-taking) from dominants, usually among females (pay-for-infant-access hypothesis) (Maestripieri, 1994): this strategy is common in Old World monkeys, e.g. female long-tailed macaques (Gumert, 2007), baboons (Frank and Silk, 2009; Henzi and Barrett, 2002), Golden Snub-Nosed Monkeys (Wei et al., 2013), patas monkeys (Muroyama, 1994), and vervet monkeys (Fruteau et al., 2011), and occurs also in capuchins (Tiddi et al., 2010). Payment for infant-access is typically not expected in cooperatively breeding species, where group members other than the mother help rearing the offspring, rather than kidnapping and eventually neglecting and abusing infants (Hrdy, 2009). However, in cooperatively breeding marmosets, contributing to infant-care is not always equally possible for all potential caretakers, because infants can only be carried by one individual at the same time, and caretakers also compete over infant-access (Mills et al., 2004; Price, 1991; Yamamoto and Box, 1997). In particular female helpers are not always tolerated to handle and carry infants, despite being strongly motivated to do so (Albuquerque, 1999), or they are allowed to carry infants only after several weeks (Finkenwirth et al., 2016). This can partly be explained by divergent reproductive tactics of male and female marmoset helpers, which under some conditions can lead to infanticidal threat emanating from helper females toward infants (Yamamoto et al., 2014). The pay-for-infant-access hypothesis thus predicts that helpers, especially females, groom their parents more than vice versa, and that grooming given from helpers to parents is positively linked to infant-access and infant-carrying. We did not expect a link with food sharing, however, because food sharing can be performed ad libitum by all individuals (Finkenwirth et al., 2016).

Finally, positive effects on individual cooperativeness may derive from the quality of the individuals' dyadic relationships themselves (relationship-quality-hypothesis). This is consistent with the results reviewed by Seyfarth and Cheney (2012), which show that strong social bonds, or friendships, often involve cooperative interactions and are adaptive. For instance, bond strength and relationship quality have been shown to predict future cooperation in agonistic coalitions and thus enhanced social dominance and paternity success (reviewed by Ostner and Schülke, 2014; van Hooff and van Schaik, 1994), e.g. in male Barbary and Assamese macaques (Berghänel et al., 2011; Schülke et al., 2010), and they improve the coordination and efficiency

of cooperative defense against predators in crested macaques (Micheletta et al., 2012). Furthermore, in chimpanzees, bonding facilitates the sharing of information via food-associated calls (Slocombe et al., 2010) and cooperation during hunting (Stanford et al., 1994), food sharing (Boesch and Boesch, 1989), and territory defense (Goodall et al., 1979). Overall, social bonding is thus associated with fitness benefits, including decreased mortality risk and increased life span in humans and non-human primates (Holt-Lunstad et al., 2010; Silk et al., 2010), and increased reproductive success (infant survival, shorter birth intervals) (Kapsalis, 2004; Palombit et al., 1997; Silk et al., 2003; Silk et al., 2009; Smuts, 1985). In cooperatively breeding primates, strong social bonds may thus well translate into increased cooperation during infant-care. The relatively higher mutual grooming levels in breeders of cooperatively breeding tamarin monkeys during pregnancy (Löttker et al., 2007) may in fact well reflect mutual investment to enhance cooperation during care-taking after infant-birth. However, positive consequences of high dyadic relationship quality on cooperativeness during infant-care in group-living callitrichids, such as marmosets and tamarins, have not been investigated so far. To test the relationship-quality hypothesis in marmosets, we therefore predicted that high quality relationships between mate pairs and potentially in some breeder-helper dyads (e.g. in dyads that are most important during infant-care) is positively linked to individual care-taking contribution after birth. Furthermore, in contrast to both strategic grooming hypotheses (pay-for-help and pay-for-infant-access), the relationship quality hypothesis predicts that grooming given to a partner is positively correlated to care-taking contribution of the groomer, possibly reflecting increased prosocial motivation in both breeder-breeder dyads and in breeder-helper dyads.

To test the predictions of the three hypotheses (table 5.1), we studied five family groups of captive marmosets over a total of eight reproductive events. We recorded directed grooming and mutual dyadic affiliation before and after birth. Individual cooperativeness was estimated based on infant-carrying and food sharing after infant-birth.

Potential effects of strategic grooming as payment for help or infant-access were assessed separately for the pre- and post-birth period. Potential effects emanating from pre-birth grooming would precede the actual helping situation and may thus rather be related to relationship management than direct payment, whereas potential effects of post-birth grooming are more likely to be associated with more proximate mechanisms including tension reduction or tactical behavior. The presence of infants in the post-partum period may thus evoke specific behavioral

changes among caretakers that we aim to capture with the separated analysis. To assess the influence of relationship quality on individual care-taking contribution, we only used the pre-birth period to quantify relationship quality because post-birth affiliation occurs in the presence of infants and may thus rather reflect behavioral interactions that are directly related to infant-handling, care-taking, or strategic behavior (hypothesis 1 and 2 in table 5.1). Furthermore, the relationship structure of marmoset family groups has been shown to be stable for at least six months (chapter 3, Finkenwirth and Burkart, in preparation-b).

5.3. Methods

5.3.1. Study animals

We observed five marmoset groups (26 individuals) during eight reproductive events over six to 12 weeks, starting one week prior to birth. In two reproductive events, observations only started with infant-birth, hence pre-partum analyses are based on six reproductive events. Reproductive event order, group identity, and individual sex and status of all studied individuals are listed in supplementary table S 5.2. Ten individuals from two groups were sampled repeatedly during different reproductive events, however only five individuals from one group (Lancia) also occurred repeatedly in the analysis of pre-birth behavioral effects, since for the other group (Nina) no pre-birth behavioral data were available in the second and third sampling period.

All groups were housed in standardized enclosures (depending on group size, one or multiple basic cage units; each measuring 2.4 m height x 1.5 m depth x 0.8 m width). All enclosures were connected to spacious outdoor areas and equipped with a sleeping box, a water dispenser, several wooden climbing structures, an infrared lamp and a mulch floor. The animals were housed under natural light with additional artificial light on a 12 h/12 h light–dark cycle and UV light (300W). Their diet consisted of a vitamin and calcium-enriched porridge in the morning, fresh fruits and vegetables over midday, as well as gum and mealworms in the afternoon, and water was available ad libitum.

5.3.2. Behavioral observations

During each reproductive event, we observed dyadic affiliation (grooming and huddling) among adult marmoset group members. Agonistic interactions were rare and therefore not analyzed in the present study. Directed grooming (picking the fur or skin of a partner with hands or mouth) levels and mutual huddling (resting in direct body contact) were recorded as all occurrences, based on either group scans (birth 1-4) or continuous observations (birth 5-8). Group scans were performed three times per week for each group, recording all dyadic affiliative interactions for all group members over two hours every five minutes (24 scans per observation day and group). Continuous observations were performed three times per week (between 9–12 am or 1–5 pm) for each group during group focal observations of 50-60 minutes per group (10 minutes for each group member), in which specific dyadic affiliative interactions among all group members were recorded. All observed behaviors were corrected for observation time or the number of scans, respectively. All measures of affiliation were z-transformed prior to analyses in order to eliminate potential variation in absolute values emanating from the different recording methods in birth 1-4 and 5-8. To assess the effects of dyadic-specific relationship quality on individual care-taking, we estimated mutual dyadic affiliation as indicator of relationship quality for each dyad. To do so, we combined mutual grooming and huddling into one mutual affiliation value per dyad, by summing up the frequencies of each behavior prior to z-transformation.

For each individual, infant-carrying was recorded daily between 8 am and 5 pm in hourly group scans during 100 days after birth. Food sharing, including proactive and reactive sharing, was assessed experimentally as described in Finkenwirth et al. (2016) and Martins et al. (in preparation). During the postpartum study period, we tested each individual two to three times per week (between 9–12 am or 1–5 pm), by presenting five food items one after another to the specific individual, and recording the frequencies and characteristics of sharing (direction, vocalizations, begging intensity, pro- and reactivity). Carrying is expressed as percentage of the total number of scans (100*scans carried/total scans) and food sharing as percentage of shared food items relative to the total number of food items received.

5.3.3. Statistical analyses

We investigated the influence of strategic grooming and dyadic relationship quality (mutual affiliativeness) on individual cooperativeness (infant-carrying and food sharing) in reproductive marmoset groups.

First, in part a), we tested whether directed grooming was used strategically as payment for help from mothers to fathers and from parents to helpers (pay-for-help hypothesis). To do so, we tested whether grooming (without infants involved) in the pre- and post-birth period was more directed from mothers to fathers than vice versa and from parents (mothers and fathers) to helpers than vice versa, using Wilcoxon Signed Ranks Test. We then tested whether grooming received from fathers by mothers and from helpers by parents was positively linked to infant-carrying or food sharing in fathers and helpers (grooming recipients), respectively. To do so, we performed permutation Spearman correlations with bootstrapping, which allowed us to control for dyadic dependencies in the data and for the repeated occurrence of individuals that were sampled twice in different reproductive events.

Second, in part b) we tested whether directed grooming was used strategically as payment for infant-access from helpers to parents (pay-for-infant-access hypothesis). We tested whether grooming in the pre- and post-birth period was more directed from helpers to parents than vice versa, using Wilcoxon Signed Ranks Test. We then tested whether grooming given from helpers to parents was positively linked to infant-carrying in helpers (grooming donors), using permutation Spearman correlation.

Third, in part c), we tested whether pre-birth dyadic relationship quality (mutual dyadic affiliation) had positive effects on care-taking of breeders in breeding pairs or of breeders and helpers in breeder-helper dyads. To do so, we correlated dyadic mutual affiliation values from breeding pairs with individual food sharing and infant-carrying rates of breeders, and dyadic affiliation values from mother-helper and father-helper dyads with food sharing and infant-carrying rates of breeders and helpers, using permutation Spearman correlations. We furthermore tested whether non-strategic grooming is linked to more helping in the groomer, i.e. whether more affiliative individuals are also more cooperative. To do so, we correlated grooming given by breeders to their mate and between breeders and helpers with the groomers' infant-carrying and food sharing levels, respectively.

5.4. Results

a) Pay-for-help hypothesis

Breeder-breeder dyads – do mothers pay fathers for help?

In contrast to the prediction, mothers did not groom fathers more than vice versa. Rather, we found a trend in the opposite direction before birth (Z=-1.78, p=0.075, N=6) and no difference after birth (Z=-1.26, p=0.208, N=6). Consistent with the pay-for-help hypothesis, pre-birth grooming by mothers to fathers was indeed positively linked to infant-carrying by fathers (Rho=0.83*, p=0.042, N=6), but the same effect was also found for the opposite direction, i.e. pre-birth grooming by fathers was positively linked to infant-carrying by mothers (Rho=0.89*, p=0.019, N=6). Hence, both fathers and mothers are more engaged in infant-carrying when they receive more grooming from their mate before birth, and this effect was particularly strong when mothers and fathers were combined in the analysis (Rho = 0.83**, p= 0.001, N=12, figure 5.1 A). This result is not consistent with the pay-for-help hypothesis, but it supports the relationship-quality hypothesis. Furthermore, pre-birth grooming from mothers to fathers had a positive effect on food sharing in fathers (Rho=0.83*, p=0.042, N=6), whereas fathers grooming mothers had no effect on mothers' food sharing (Rho=0.54, p=0.266, N=6) (figure 5.1 B). No effect was found for post-birth grooming from mothers to fathers (and vice versa) on either infant-carrying (fathers: Rho=0.10, p=0.823, N=8; mothers: Rho=-0.12, p=0.779, N=8) or food sharing (fathers: Rho=0.52, p=0.183. N=8; mothers: Rho=-0.33, p=0.420, N=8) of the recipients.

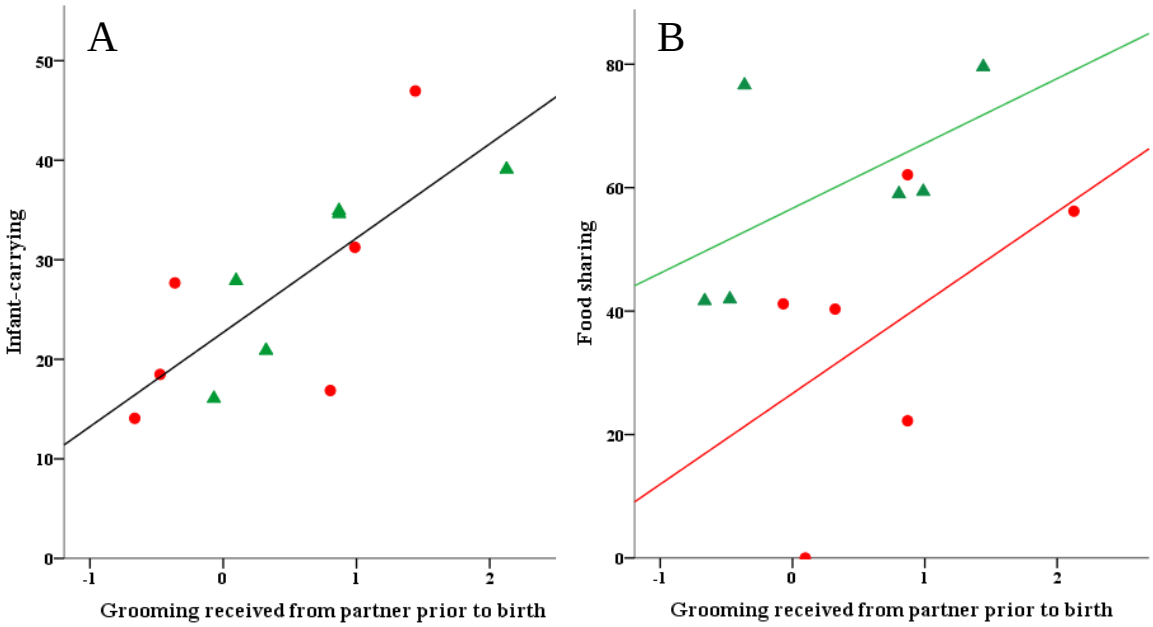

Figure 5.1: Positive link between grooming received and care-taking contribution. Grooming *received* from the partner prior to birth in marmoset breeders is positively linked to infant-carrying (A, % of total time observed) in breeder females (red circles) and males (green triangles) (Rho = 0.83**, p= 0.001, N=12), and to food sharing (B, % of total items shared) in males (Rho=0.83*, p=0.042, N=6), but not females (Rho=0.54, p=0.266, N=6).

Breeder-helper dyads – do parents pay helpers for help?

Grooming directions and effects of directed grooming on care-taking in helpers was analyzed separately for mother-daughter, mother-son, father-daughter, and father-son dyads. Mothers did not groom daughters and sons more than vice versa (daughters: pre-birth: Z=-0.09, p=0.929, N=11; post-birth: Z=-0.72, p=0.469, N=16; sons: pre-birth: Z=-1.01, p=0.314, N=9; post-birth: Z=-1.41, p=0.158, N=14). Fathers also groomed neither daughters nor sons more (daughters: pre-birth: Z=-1.60, p=0.109, N=11; post-birth: Z=-0.827, p=0.408, N=16; sons: pre-birth: Z=-1.25, p=0.213, N=9; post-birth: Z=-1.73, p=0.084, N=14). However grooming towards all helpers combined was significantly higher from fathers to helpers than vice versa before birth (Z=-2.09, p=0.036, N=20), whereas a trend for the opposite effect was found for fathers after birth, as helpers groomed fathers more than vice versa (Z=-1.78, p=0.075, N=30), but not for helpers grooming mothers (Z=-2.98, p=0.766, N=30).

The grooming patterns thus partially correspond to the predictions of the pay-for-help hypothesis. However, we found no evidence that grooming from breeders increased infant-care contribution of helpers, since neither pre-birth nor post-birth directed grooming from breeders to helpers had a positive effect on helpers' infant-carrying or food sharing (supplementary table S 5.3). Rather, there was a negative effect of pre-birth grooming by fathers on post-birth food sharing in helpers (Rho=-0.51, p=0.031, N=18), especially in daughters (Rho=-0.69, p=0.026, N=10).

b) Pay-for-infant-access hypothesis

Breeder-helper dyads - Do helpers pay parents for access to infants?

Helpers did not groom their parents more than vice versa before birth (see results in part a). After birth, there was a trend for more grooming from helpers towards fathers than vice versa, but only if both females and males were combined (Z=-1.78, p=0.075, N=30; see also results part a), which is consistent with the pay-for-infant-access hypothesis. Nonetheless, neither pre- nor post-birth grooming by helpers to parents was linked to infant-carrying in helpers after birth (helper females grooming breeder females: pre-birth: Rho=-0.41, p=0.235, N=10; post-birth: Rho=-0.08, p=0.794, N=14; helper females grooming breeder males: pre-birth: Rho=-0.25, p=0.483, N=10, post-birth: Rho=0.09, p=0.742, N=14; helper males grooming breeder females: pre-birth: Rho=0.14, p=0.736, N=8; post-birth: Rho=0.02, p=0.957, N=12; helper males grooming breeder males: pre-birth: Rho=0.14, p=0.736, N=8; post-birth: Rho=0.48, p=0.114, N=12).

c) Mutual dyadic relationship quality hypothesis

Breeder-breeder dyads

When testing the effect of dyadic relationship quality (based on *mutual dyadic affiliation*) on individual care-taking contribution in breeders, we found that dyadic affiliation from the pre-birth period was positively related to infant-carrying in both breeder females (Spearman's rank correlations: Rho=0.89*, p=0.019, N=6) and males (Rho=0.83*, p=0.042, N=6). This effect was particularly strong when females and males were combined in the analysis (Rho=0.79**, p=0.002, N=12, figure 5.2). For food sharing, no such effect was found over all breeders

combined (Rho=0.45, p=0.140, N=12) or in females (Rho=0.31, p=0.544, N=6), but we found a strong positive trend in males (Rho=0.77, p=0.072, N=6).

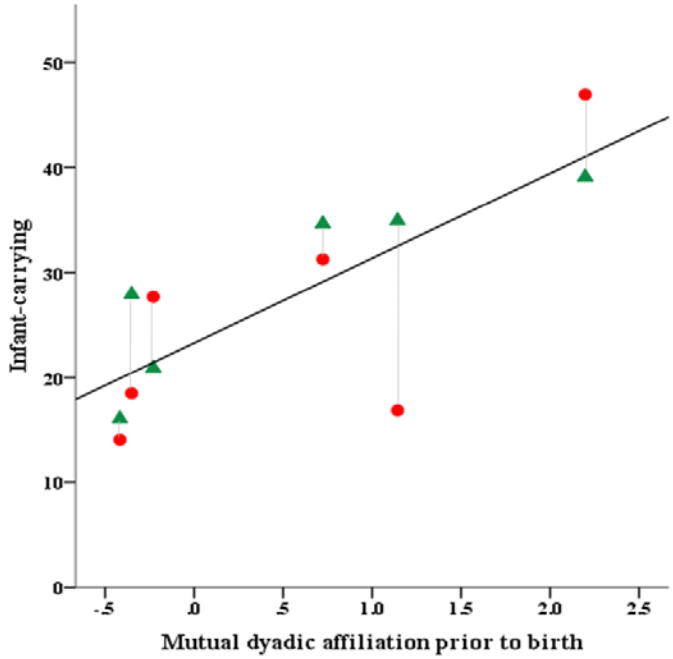

Figure 5.2: Positive link between mutual dyadic affiliation and infant-carrying. Pre-birth *mutual dyadic affiliation* among marmoset breeders is positively linked to the level of infant-carrying (% of total time observed) in both females (red circles) and males (green triangles) (Rho = 0.83**, p= 0.001, N=12). Dotted lines connect breeding pairs.

Furthermore, we tested whether more affiliative individuals are also more cooperative. We found that the amount of grooming *given* to the partner prior to birth was positively correlated with the groomer's contribution to infant-carrying (Rho = 0.734**, p=0.007, N=12; figure 5.3A) and food sharing (Rho = 0.727**, p= 0.007, N=12; figure 5.3B) after birth. These effects are still present for carrying, if analyzed separately for females (Rho=0.89*, p=0.019, N=6) and males (Rho=0.83*, p=0.042, N=6), but weaker for food sharing, where the effect remains significant in males (Rho=0.83*, p=0.042, N=6) but not in females (Rho=0.54, p=0.266, N=6).

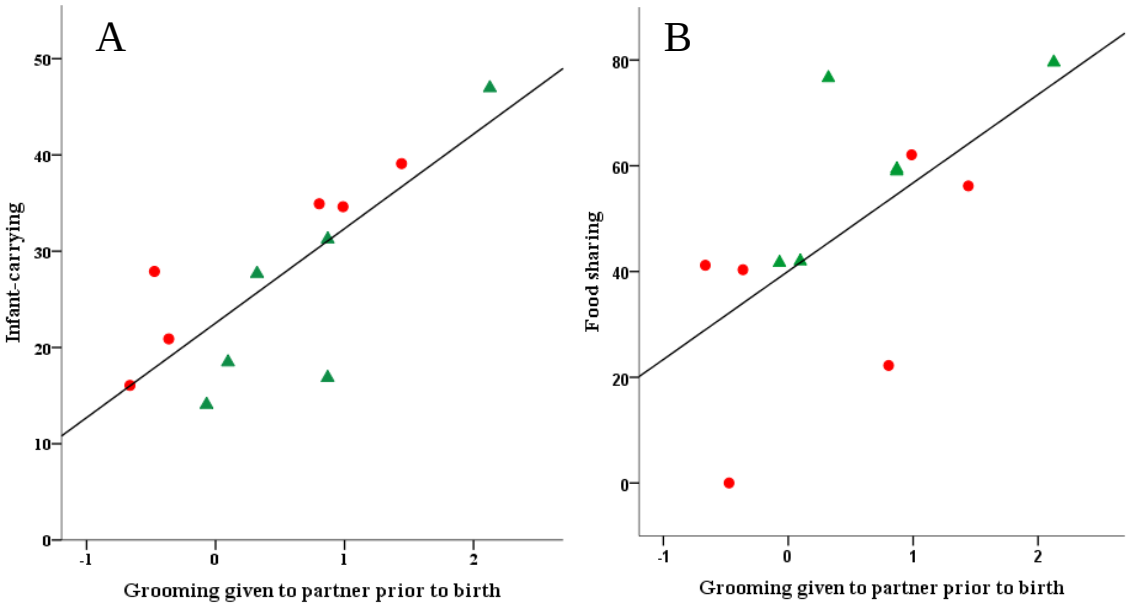

Figure 5.3: Positive link between grooming given to partner before birth and care-taking contribution. Pre-birth grooming *given* by female (red circles) and male (green triangles breeders towards their mates is linked to infant-carrying (A, Rho = 0.73**, p=0.007, N=12) and food sharing (B, Rho = 0.73**, p= 0.007, N=12).

Breeder-helper dyads

Looking at specific effects of breeder-helper relationship quality on breeder and helper cooperativeness, we found a positive effect in male helpers. Specifically, helper males shared more food after birth when they shared higher pre-birth levels of *mutual dyadic affiliation* with their mothers (Rho=0.81*, p=0.015, N=8, figure 5.4), but not with their fathers (Rho=-0.04, p=0.933, N=8).

In contrast, infant-carrying of male helpers was not associated with pre-birth affiliation with mothers or fathers, and we found no evidence for a link between pre-birth mutual affiliation and care-taking behaviors in female helpers or breeders (supplementary table S 5.4). When analyzing the link between grooming *given* before birth and the groomers' cooperativeness, we found that fathers who groomed their sons more also carried more after birth (Rho=0.76*, p=0.019, N=8). This link was also reflected over all helpers, i.e. fathers' carrying was correlated with their grooming towards all helpers (Rho=0.51, p=0.029, N=18). A positive link was furthermore found between grooming *given* from sons to mothers and food sharing in sons

(Rho=0.83*, p=0.010, N=8) and this link was also reflect in a positive effect over all helpers (Rho=0.54, p=0.022, N=18). All other dyadic combinations did not show an effect of grooming given on care-taking behavior of the groomer (supplementary table S 5.4).

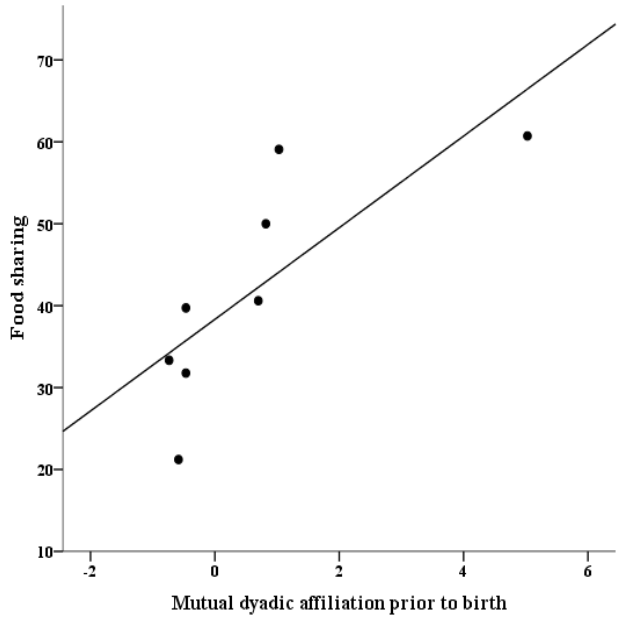

Figure 5.4: Positive link between mutual dyadic affiliation before birth and food sharing. Pre-birth *mutual dyadic affiliation* between mothers and male helpers is positively linked to food sharing of male helpers (Rho=0.81*, p=0.015, N=8).

5.5. Discussion

The aim of this study was to assess how dyadic relationships and directed grooming between adult group members influence the contribution to infant-care in cooperatively breeding common marmosets. In particular, we tested the pay-for-help hypothesis, the pay-for-infant-access hypothesis, and the relationship quality hypothesis.

According to the pay-for-help hypothesis, breeding females are expected to groom breeding males more than vice versa, and males should contribute more to infant-care the more grooming they receive. Likewise, it predicts that breeders of both sexes groom helpers more as incentive to help. We indeed found that fathers who received more grooming from their mates before birth engaged more in infant-carrying and food sharing, but unlike as predicted, the same effect was also found in mothers, who likewise carried more if they had received more grooming

from fathers prior to birth. Fathers, but not mothers, groomed helpers more in the pre-birth period, but grooming from breeders to helpers had no positive effect on care-taking in helpers. Rather, we found a weak negative effect. Together, these results do not support the pay-for-help hypothesis.

According to the pay-for-infant-access hypothesis, helpers, especially females, are expected to groom their parents more than vice versa before and after birth, and grooming given to parents should be positively linked to infant-carrying in helpers. We found no evidence to support this hypothesis, since neither pre- nor post-birth grooming was more directed from helpers to parents than vice versa. Likewise, grooming from helpers to parents in both periods was not associated with more infant-access (i.e. carrying) by helpers after birth. The same was also true when only looking at female helpers, who are most likely to have restricted access to infants.

Finally, according to the relationship-quality-hypothesis, pre-birth dyadic mutual affiliation is expected to positively influence individual care-taking contribution in both partners, both in breeding pairs and breeder-helper dyads. Positive evidence for this hypothesis was found in breeders, since both females and males engaged equally in grooming prior to birth, and both carried infants more and shared more food after birth when they were engaged in highly affiliative relationships with their mates. Moreover, breeders of both sexes who groomed their partners more prior to birth also contributed more to care-taking behavior once the infants were born (food sharing and infant-carrying), suggesting that intrinsic prosocial motivation may significantly contribute to high dyadic relationship quality. Furthermore, similar albeit weaker effects were found in dyads including parents and sons: sons shared more food after birth when they were engaged in more affiliative relationships with their mothers and when they groomed their mothers more before birth, and fathers who groomed their sons more before birth, contributed more to infant-carrying.

Overall, our findings do not support the pay-for-help and pay-for-infant-access hypotheses, because they suggest that relationship quality rather than strategically directed grooming is linked to cooperativeness in marmoset caretakers. These findings are consistent with increased grooming levels during pregnancy in both breeding partners in tamarins (Löttker et al., 2007). Nevertheless, in breeder-helper dyads, grooming rates have been reported to be on average more directed from breeders to helpers than vice versa (Lazaro-Perea et al., 2004). This

was also the case for the marmoset fathers in the present study (but not for mothers), but receiving more grooming pre- or post-birth from fathers or mothers did not increase contributions to care-giving in the helpers. This pattern may reflect that breeders invest more in the maintenance of overall within-group cohesion and cooperation, since this directly determines their reproductive success (status differences in grooming rather apply on the group level). When looking specifically at female-female dyads, Lazaro-Perea et al. (2004) found that dominant individuals were more likely to groom non-breeding individuals. However, these authors suggest that received grooming from mothers does not facilitate care-taking contribution in female helpers but may rather relate to other services like territorial defense, in which female helpers participated particularly much in the respective study. To some degree, our findings also stand in contrast to earlier findings by Ginther and Snowdon (2009), showing a positive link between maternal grooming and previous carrying contribution in sons. However, this study did not investigate potential effects of directed grooming on future helping in sons, and, together with our findings, they suggest that grooming from mothers to sons may be more relevant as a feedback and subsequent reward to the previous performance than as preceding payment for help during the prospective breeding season. Furthermore, fathers even groomed sons more if they were previously less engaged in care-taking, possibly to prepare unexperienced sons for their social role as caretakers. The authors suggest that, on the proximate level, greater comfort and physical contact among caretakers may thereby be more rewarding than specifically directed grooming (Ginther and Snowdon, 2009; Price, 1992).

The positive effect of relationship quality in breeding pairs was consistently reflected in pre-birth dyadic affiliation but also in pre-birth directed grooming levels, that were linked to helping in groomers as well as grooming recipients. These findings indicate that mothers do not simply use grooming as incentive for fathers to help but that both parents “reassure” and strengthen their bond mutually prior to birth, which is associated with higher parental investment in infant-care. Accordingly, consistent with the relationship hypothesis, this effect was equally strong in females and males. In addition to relationship quality, individual differences in intrinsic prosocial motivation may also contribute to our pattern of results. This applies in particular to the finding that more affiliative individuals were also more cooperative, i.e. that grooming given was correlated with the groomers’ cooperativeness (both infant-carrying and food sharing). In support of this assumption, mean individual infant-carrying and food sharing was also correlated over all

individuals in the eight reproductive events (Rho=0.04, p=0.035, N=41). Thus, the link between relationship quality and cooperativeness may arise because individuals who are more motivated to invest in high quality relationships are also more motivated to engage in infant-care.

Interestingly, the positive effect of relationship quality was specifically found for breeding pairs and male helpers, who are the most important caretakers in marmoset groups (Digby et al., 2007; Goldizen, 1987b; Koenig and Rothe, 1991). Our recent findings in Finkenwirth et al. (2015) suggest that group-living marmosets form differentiated dyadic relationships that are stable for at least six months (chapter 3, Finkenwirth and Burkart, in preparation-b). Hence, this indicates that the maintenance of high quality relationships may be an important basis for successful cooperation during infant-care, not only in breeding pairs but also between breeders and other main caretakers in marmoset groups.

Female helpers, even though presumably highly motivated, contribute considerably less to infant-carrying, whereas both female and male helpers show equally high levels of food sharing when infants are present (Finkenwirth et al., 2016). This raises the question, why relationship quality between breeders and female helpers was not associated with food sharing in female helpers like in males. Interestingly, our data even indicate that daughters share less food when they received more directed grooming from fathers before birth, which stands in contrast to the pay-for-help and relationship-quality-hypotheses and the findings in mother-son dyads. Thus, further studies are required to investigate the role of relationship quality and potential adaptive value of differentiated relationships on cooperativeness in marmoset groups in more detail, with specific focus on sex-specific differences in helpers.

5.6. Acknowledgements

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5.7. Supplementary material

Table S 5.2: Data sampling protocol. Table listing the order and behavioral sampling protocol of eight reproductive events (RE) as well as individual group membership, name, sex, and status of all 14 individuals that were part of this study.

RE	group	individual	status	sex	Behavioral observations	
					Pre-birth	Post-birth
1	Lancia	Lancia	breeder	female	yes	yes
		Lexus	breeder	male	yes	yes
		Lea	helper	female	yes	yes
		Larissa	helper	female	yes	yes
		Leon	helper	male	yes	yes
2	Mina	Mina	breeder	female	yes	yes
		John	breeder	male	yes	yes
		Mibba	helper	female	yes	yes
		Membo	helper	male	yes	yes
3	Nina	Nina	breeder	female	yes	yes
		Lex	breeder	male	yes	yes
		Nigg	helper	male	yes	yes
		Nari	helper	male	yes	yes
		Nala	helper	female	yes	yes
4	Nina	Nina	breeder	female	no	yes
		Lex	breeder	male	no	yes
		Nigg	helper	male	no	yes
		Nari	helper	male	no	yes
		Nala	helper	female	no	yes
5	Lancia	Lancia	breeder	female	yes	yes
		Lexus	breeder	male	yes	yes
		Lea	helper	female	yes	yes
		Larissa	helper	female	yes	yes
		Leon	helper	male	yes	yes
6	Jojoba	Jojoba	breeder	female	yes	yes
		Marvin	breeder	male	yes	yes
		Jet	helper	male	yes	yes
		Jupi	helper	female	yes	yes
		Jaja	helper	female	yes	yes
7	Kuta	Kuta	breeder	female	yes	yes
		Jossua	breeder	male	yes	yes
		Kos	helper	male	yes	yes
		Kossa	helper	female	yes	yes
		Kossua	helper	female	yes	yes
		Kossu	helper	male	yes	yes
8	Nina	Nina	breeder	female	no	yes
		Lex	breeder	male	no	yes
		Nigg	helper	male	no	yes
		Nari	helper	male	no	yes
		Nala	helper	female	no	yes
		Nikita	helper	female	no	yes

Table S 5.3: Effects of pre- and post-birth grooming from parents to helpers on helper infant-carrying and food sharing, respectively.

Interaction	N dyads	Carrying by helpers		Food sharing by helpers		
		Rho	p	n	Rho	p
Grooming in pre-birth period:						
Mother grooming all helpers	18	0.19	0.456	18	0.29	0.231
Mother grooming daughters	10	0.19	0.610	10	0.22	0.538
Mother grooming sons	8	0.33	0.420	8	0.26	0.531
Father grooming all helpers	18	-0.31	0.205	18	**-0.51**	**0.031**
Father grooming daughters	10	-0.47	0.168	10	**-0.69**	**0.026**
Father grooming sons	8	0.36	0.382	8	0.16	0.713
Grooming in post-birth period:						
Mother grooming all helpers	26	-0.31	0.126	26	-0.25	0.227
Mother grooming daughters	14	0.02	0.935	14	-0.50	0.085
Mother grooming sons	12	-0.90	0.778	12	0.14	0.656
Father grooming all helpers	26	-0.12	0.571	26	-0.04	0.843
Father grooming daughters	14	-0.22	0.453	14	0.14	0.640
Father grooming sons	12	-0.10	0.752	12	0.06	0.853

Table S 5.4: Effects of pre-birth mutual affiliation and grooming given on infant-carrying and food sharing of both partners and of the groomer, respectively, in breeder-helper dyads.

Inter-action	dyad type	N dyads	Carrying by				Food sharing by			
			breeders		helpers		breeders		helpers	
			Rho	p	Rho	p	Rho	p	Rho	p
Mutual affiliation before birth	Mother - helpers	18	0.10	0.681	0.42	0.079	0.02	0.942	0.439	0.068
	Mother - daughters	10	0.10	0.787	0.22	0.544	-0.06	0.866	0.10	0.789
	Mother - sons	8	0.17	0.690	0.21	0.610	0.07	0.865	**0.82**	**0.015**
	Father - helpers	18	0.38	0.116	-0.09	0.717	0.12	0.631	0.08	0.744
	Father - daughters	10	0.23	0.517	0.18	0.627	-0.09	0.813	0.26	0.467
	Father - sons	8	0.49	0.223	0.18	0.670	0.32	0.447	-0.04	0.933
Grooming given before birth	Mother - helpers	18	-0.03	0.901	0.09	0.723	-0.06	0.346	**0.54**	**0.022**
	Mother - daughters	10	-0.12	0.745	-0.41	0.235	0.45	0.192	0.09	0.789
	Mother - sons	8	0.06	0.887	0.14	0.736	0.42	0.298	**0.83**	**0.010**
	Father - helpers	**18**	**0.51**	**0.029**	-0.06	0.819	0.36	0.141	0.09	0.713
	Father - daughters	10	0.43	0.217	-0.25	0.483	0.40	0.247	0.35	0.322
	Father - sons	8	**0.76**	**0.019**	0.14	0.736	0.44	0.280	-0.07	0.867

6. General discussion and outlook

In my PhD Thesis, I investigated the role of OT in the regulation of social relationships and individual cooperativeness in group-living common marmosets, and, taken together, how this explains individual variation in prosocial behaviors. My results capture OT effects at the dyadic level with regard to social bonding, at the individual level with regard to care-taking behavior, and at that of the interaction of these two with regard to the effects of bonding on individual care-taking. First, I could show that across all dyad types, marmosets engage in differentiated relationships, characterized by high levels of dyadic affiliation and dyadic OT synchrony between strongly bonded partners (chapter 2). Second, stable patterns of dyadic affiliation, dyadic OT synchrony, and individual group integration over two distinct sampling periods indicate that the differentiated relationship structure and individual social positions in marmoset groups are stable for at least six months (chapter 3). Together, these findings suggest that not only marmoset breeders but also other individuals engage in selective social relationships with preferred grooming partners. Furthermore, I found that individual variation in prosocial infant-care behavior is reflected in peripheral OT levels, i.e. specifically care-taking behaviors that reflect high intrinsic prosocial motivation are strongly positively linked to OT (chapter 4). Finally, chapter 5 shows that the differentiated relationships in marmosets found in chapters 2 and 3 are also relevant to understand individual variation in prosociality and cooperativeness, since high-quality relationships positively affected infant-care behavior. Specifically, I found that breeders and male helpers, who are the main caretakers in marmoset groups, contributed more to infant-care when they were engaged in relationships of higher quality, whereas my findings do not support the assumption that strategically directed grooming may be used as incentive to pay others for help or for infant-access.

Overall, I could show that investigating peripheral OT patterns and social relationships in marmoset family groups provides meaningful insight into the constraints and flexibility that shape individual prosociality in common marmosets, and thus, into the proximate regulation of marmoset cooperative group life. My findings thereby give an impression on the complex role of OT in the highly interdependent and cooperative but also flexible social systems of callitrichid monkeys. Moreover, they provide a solid basis for future studies that may further explore the coordination and interaction of OT effects with regard to prosociality in humans and non-human primates.

6.1. OT mediating social bonding – the OT feedback-loop model

My results are generally consistent with earlier findings that report a positive link between urinary OT levels and positive social interactions in callitrichid monkeys, e.g. with regard to affiliative and socio-sexual interactions in tamarin mate pairs (Snowdon et al., 2010), and to visual, olfactory, and affiliative contact in marmoset mate pairs after separation (Seltzer and Ziegler, 2007). However, I could qualify these findings because, at least in marmoset family groups, urinary OT levels are not simply positively linked to affiliative interactions in an unspecific manner. Rather, positive OT effects are captured in partner-specific patterns, since affiliation with strongly bonded partners but not with non-bonded partners influences individual urinary OT levels. As a result, strongly bonded partners show synchronized OT levels over time (chapter 2), and these partner-specific patterns are consistent over at least six months (chapter 3). This directly ties in with partner-specific OT effects, related to dyadic grooming and food sharing, that Crockford et al. (2013) and Wittig et al. (2014) reported from wild chimpanzees. When taken together, these findings suggest that, in primates, OT mediates social bonding also among non-sexual partners, and that partner-specific OT responses to affiliative interactions may provide a non-cognitive mechanism of book-keeping of an individual's relationships with other group members (Crockford et al., 2013). Bonds may thus rather be built under the influence of emotional and motivational amplification (also see section 6.2.) than through strategic calculations. Recent evidence from humans indeed shows that social bonding (and cooperation) are associated with increased emotional attachment (Baumeister and Leary, 1995) and trust (Larzelere and Huston, 1980) between partners, which, to some degree, also seems to be the case in other primates (Schino and Aureli, 2009).

At the proximate level, the bilateral relations between bond-enhancing behaviors and bond strength may be regulated via a positive feedback-loop that amplifies partner-specific OT responses due to repeated affiliative and prosocial interactions between two individuals (figure 6.1). Over time, the changing valence of a strengthening bond may thus be reflected in increased OT release in response to affiliative interactions, and partner-specific OT elevation may in turn facilitate cooperative interactions among these partners. Hence, rather than simply amplifying affiliative and cooperative behavior in an unspecific manner, OT itself seems to allow to set relationships and social interactions into context. This similarly applies to chimpanzees and

callitrichid monkeys, and may thus also be relevant for humans, who are thought to incorporate the high cognitive abilities of great apes and increased prosociality due to cooperative breeding (Burkart et al., 2009). Nonetheless, the neurological pathways involved and adaptive functions of social bonds may differ in these species.

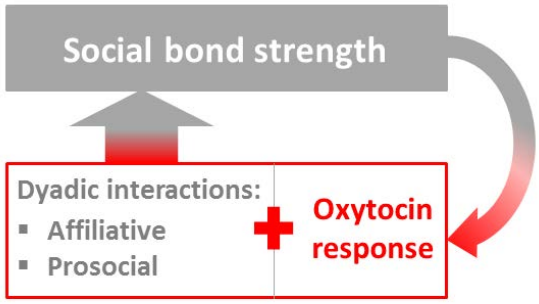

Figure 6.1: Scheme of a positive OT feedback-loop, mediating social bond strength through bond-enhancing behaviors and increasing oxytocin responses.

6.2. Integrating positive effects of OT and social bonding on prosocial infant-care

My findings in chapters 4 and 5 show that the combination of hormonal and behavioral monitoring provides valuable insight into the regulation of prosocial behavior during infant-care in group-living marmosets: Care-taking behavior is positively linked to the caretakers' OT levels as well as to the quality of their relationships with other group members. Interestingly, the positive effect of OT occurred only in association with prosocial behaviors that are particularly prone to reflect high levels of intrinsic motivation (infant-licking and proactive food sharing), but not linked to behaviors that are characterized by intense physical body contact but that cannot be performed ad libitum (infant-grooming and –carrying). The positive OT effects related to infant-licking and proactive food sharing occurred successively in early and late infancy, thus directly reflecting the changing needs of the growing infants. Furthermore, especially breeders but also adult sons, which are the main caretakers in marmoset groups, contributed more to infant-care when they were engaged in better relationships with increased mutual affiliation and directed grooming between both partners.

Altogether, these findings point to an interrelation of positive OT effects related to bonding and individual prosocial behavior, especially since OT is also crucially involved in the regulation of social bonding. Thus, the positive OT feedback effects on intrinsic prosocial motivation characteristic of high-quality relationships and intense affiliative interactions among bonded partners may thus indirectly facilitate prosocial and cooperative behavior in the individuals involved (Uvnäs-Moberg, 1998). This feedback may also involve the joint activation of reward-stimulating brain areas and associated neuronal pathways, since OT has been shown to act as a social reinforcement signal in the nucleus accumbens through coordinated activity with serotonin (Dolen et al., 2013). The finding that exogenous OT application facilitates prosocial donations and trust even among human strangers in economic game settings (Kosfeld et al., 2005; Zak et al., 2007) reveals a potential of OT to mimic the presence of a strongly bonded partner, and thus supports the assumption that positive OT effects related to bonding and individual prosociality are intertwined. This social context-dependency may be particularly important to interpret experimental OT effects on prosocial performance, and to better understand the overall role of OT in the regulation of prosociality.

6.3. Psychological effects of OT related to cooperative breeding - Implications for humans

OT is fundamentally involved in the regulation of mammalian sociality. The diverse OT effects in the literature indicate that central OT effects and pathways grew more complex during the evolution of more complex social systems. This is particularly relevant in cooperatively breeding species like callitrichids and humans (Carter, 2014), where individuals show uniquely high levels of social tolerance and prosocial motivation toward each other, and high within-group cooperation is mandatory for reproductive success and survival (Hrdy, 2007 & 2009; Jaeggi et al., 2010).

Among primates, callitrichids and humans are the only cooperative breeders. Beside a highly cooperative life-style, they are also thought to share convergent psychological and socio-cognitive traits (Burkart et al., 2014; van Schaik and Burkart, 2010). For this reason, we recently discussed the usage of marmosets as model species to investigate socio-cognitive and neuroendocrine mechanisms that may have shaped the uniquely high levels of prosociality in humans (Burkart and Finkenwirth, 2014). Both humans and callitrichids show strong social

attentional biases, e.g. toward visual stimuli (gazes) and the actions of other group members, high proactive sharing of food and information, as well as complex vocal communication (reviewed in Burkart, 2009; Gray and Thompson, 2004; Snowdon, 2001; Whiten and Erdal, 2012). Such psychological abilities are particularly differentiated and complex in humans, who, on top of their prosocial traits, also possess extremely large brains and thus high general cognitive skills (Burkart et al., 2009).

A broad body of evidence supports the positive role of OT in emotional and socio-cognitive processing in primates, especially in humans: Specifically, OT enhances facial emotion-recognition (Domes et al., 2007), eye-gaze attention (Guastella et al., 2008a; also in macaques: Simpson et al., 2014), emotional reactivity (Domes et al., 2010), and memory for positive social information (Guastella et al., 2008b; Rimmele et al., 2009). Peripheral OT release correlates with the subjective experience of empathy (Barraza and Zak, 2009). OT has furthermore been shown to attenuate social stress in humans (Heinrichs et al., 2003; Kubzansky et al., 2012) and marmosets (Cavanaugh et al., 2016), and, most importantly, to increase trust in humans (Baumgartner et al., 2008; Kosfeld et al., 2005), especially towards familiar individuals (van Ijzendoorn and Bakermans-Kranenburg, 2012; but see Nave et al., 2015).

Altogether, enhanced socio-cognitive and psychological abilities and the central role of OT in their regulation may constitute a crucial basis for the development and display of increased other-regarding preferences and prosociality in callitrichids (Burkart et al., 2007) and humans (reviewed in Fehr and Fischbacher, 2003; Fehr and Rockenbach, 2004; Fehr and Schmidt, 2006), and potentially also in other cooperative breeders. This may also be reflected in the facilitating effects of exogenous OT application in experimental contexts, e.g. on food sharing in marmosets (Saito and Nakamura, 2011a), and generosity (Zak et al., 2007), charitable donations (Barraza et al., 2011), and altruistic priorities in humans (Marsh et al., 2015). Combining the evidence from humans and primates may thus allow us to better understand specific mechanisms underlying individual variation in prosocial motivation and motivational regulation related to cooperative breeding. My results offer a promising starting point for this endeavor.

6.4. Prosociality in marmosets - Conclusion and outlook

Among non-human primates, marmosets stand out with particularly high levels of prosocial behavior and cooperation, especially but not exclusively in the context of cooperative infant-care. To some degree, individual prosocial performance and motivation is dependent on an individual's sex, reproductive status, and age, as well as the composition of its social group (e.g. the number of adult helpers of both sex) (see Burkart, 2015 and Yamamoto et al., 2014 for reviews). In my PhD-Thesis, I could show that individual variation also occurs due to other influences, like the group-specific social relationship structure and individual endogenous hormonal states (which are probably also linked to each other): Both the quality of dyadic relationships and individual OT levels are positively linked to individual prosocial infant-care behavior and prosocial motivation.

Several recent reviews in humans have pointed out the need to study and interpret OT effects on prosocial behaviors against the background of the respective social context (Bartz et al., 2011; Churchland and Winkielman, 2012; Olff et al., 2013). This involves individual preconditions, such as OT receptor gene distribution (Bakermans-Kranenburg and van IJzendoorn, 2008) and the levels of proximity and aggression experienced during childhood (Carter, 2005; Feldman et al., 2010; Heim et al., 2008), and whether the interacting individuals are bonded or belong to the same group. For species other than humans, such factors have barely been studied so far. My results, however, provide new insight into this question in non-human primates, since they show that affiliative interactions lead to partner-specific patterns in individual OT levels in marmosets, and that high relationship quality facilitates individual care-taking behavior, but only in specific dyads (breeding pairs and breeder-son dyads). Thus, partner-specific OT effects may also be involved in the facilitation of infant-care behavior among bonded partners, but such cross-effects are still poorly understood and require further investigation.

Overall, my results imply that cultivating specific high-quality relationships with the main cooperation partners via affiliative interactions may increase group cohesion and stability in marmoset groups, which, in turn, may positively influence individual prosociality and overall cooperativeness in these groups. Motivational stimulation and positively amplifying feedback mechanisms via OT may be vital to promote this "cooperative spiral", especially in the context of cooperative infant-care, as outlined in the preceding paragraphs. This could also be the core

idea of an extended OT feedback-loop model, integrating within-group coherence, partner-specific bonding, and cooperative and prosocial interactions.

To further explore the parameters that shape individual prosocial performance and motivation in cooperative breeders, future studies should broaden the perspective beyond nonhuman primates, towards other species, including humans. Furthermore, they should investigate the influence of individual pre-conditions (e.g. rearing conditions), in-group/out-group effects, and other hormones that might potentially interact with OT.

7. References

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